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CONTENTS

PAGE

T. T. Macan and A. MacFadyen. The water bugs of dewponds . 175

Dennis Chitty and Helen Chitty. Canadian Arctic Wild Life Enquiry, 1939–40 184

James Fisher and George Waterston. The breeding distribution, history and population of the fulmar (*Fulmarus glacialis*) in the British Isles 204

K. Radway Allen. Studies on the biology of the early stages of the salmon (*Salmo salar*). 3. Growth in the Thurso river system, Caithness 273

D. M. Reid. The Amphipod fauna of Oldany Harbour, Sutherland 296

C. B. Goodhart. The ecology of the Amphipoda in a small estuary in Hampshire 306

John Deal. The temperature preferendum of certain insects . 323

Reviews 357

Notices of Publications on the Animal Ecology of the British Isles 363

VOLUME 10 NOVEMBER 1941 No. 2

THE WATER BUGS OF DEWPONDS

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(*With Plate 2 and 1 Figure in the Text*)

1. INTRODUCTION

DEWPONDS have attracted much attention on account of the beliefs that they remain full and even show a rise in water level during periods of drought, dew being the responsible agent, and that some of them date back to prehistoric times. Pugsley (1939) has shown the fallacy of both these beliefs. A good deal of time has been devoted to investigating how dewponds obtain their water, but, except for some observations on the snail fauna (Hurst, 1920; Reid, 1892, etc.), little work appears to have been done on their biology, although they are particularly suitable for ecological work, being uniform in general features and many in number, so that any ecological conclusions can be based on a large number of collections.

2. GENERAL FEATURES OF DEWPONDS

The purpose of dewponds is the watering of stock in districts, chiefly chalk downs, where the soil is so pervious that there is no surface water of any kind, and they are made by excavating a hollow and lining it with some impermeable material. The finished pond (Plate 2) is some 20 yd. across, commonly square in Wiltshire and circular in Sussex, with the bottom sloping evenly from the rim to the centre. The pond is usually only about half full, but the outer unsubmerged portion plays an important part as a gathering ground (Plate 2, photo 1). The secret of construction is not concerned with giving the pond those qualities which will cause dew to condense in it, as is commonly supposed, but with making a bottom which will remain watertight for many years. The original excavation is some 4 or 5 ft. deep, and it is generally lined with puddled clay covered with chalk rubble or flints to prevent the hooves of cattle piercing it, or with concrete. The ponds are usually situated so as to obtain the maximum advantage from any surface drainage in the neighbourhood and they are often connected by a drain to the nearest road. Further details are given by Martin (1915) and Pugsley (1939).

The ecological features characteristic of dewponds are small size, shallow depth, isolation, normal absence of inflow and outflow and calcareous water. They differ among themselves in the degree of pollution, the development of vegetation and the degree of permanence. Some dewponds are left unfenced, sheep and cattle being allowed to drink direct from them. If many cattle visit one of these unfenced ponds the bottom receives a good deal of dung and the consequent enrichment of the water produces so thick a population of flagellates and other Protozoa that an object submerged in the water disappears from view a few inches below the surface; the growth of rooted vegetation under such conditions is impossible. Other ponds are fenced round and the water is siphoned from them to a drinking trough, the flow being controlled by a ball tap, and in these ponds, together with those unfenced ponds which are not visited frequently by stock, soil accumulates after an interval of time and rooted vegetation becomes established (Plate 2, photo 2). In a well-kept dewpond the vegetation is removed, perhaps as often as once a year, but in many it is allowed to accumulate and fill up the pond. As the pond gets more overgrown it tends to dry out more readily.

The work of Reid (1911) and Godwin (1923) suggests that the flora of an isolated pond is largely a matter of chance and that the only generalization to be made is that the number of species present bears a relation to the length of time the pond has been available for colonization. The dewpond flora, however, does seem to depend to some extent on environmental factors. *Lemna*, for instance, is typical of ponds in which organic matter has accumulated and given rise to a foul mud. *Chara* is the commonest species in new ponds and in ponds which are cleaned out regularly; when the pond is neglected other plants, notably *Potamogeton natans*, become established and the number of species increases to a maximum. Plant growth, however, gradually fills up the pond and fluctuations in water level increase in magnitude, with the result that the true aquatics begin to disappear and amphibious forms gain a foothold.

Concrete is now commonly used to make dewponds watertight and sometimes clay, in which case the bottom is usually protected by a layer of chalk rubble; as, in addition, many ponds receive surface drainage it is unlikely that they are deficient in lime. Unfortunately it was only possible to analyse four water samples from the present series of ponds. Samples taken from ponds D 23 and D 24 in February and June 1941 show figures for temporary hardness (as determined by titration with standard acid) which, when corrected for sodium (method of Reith & Looyen, 1938), may be compared with those of Martin (1915) for temporary hardness, apparently estimated from titration with soap solution. This is done in the following table in which all hardness values are expressed as mg. per litre of calcium carbonate.

The present set of results for February are low, due to heavy rainfall, while those for June followed a dry period during which the water level fell con-

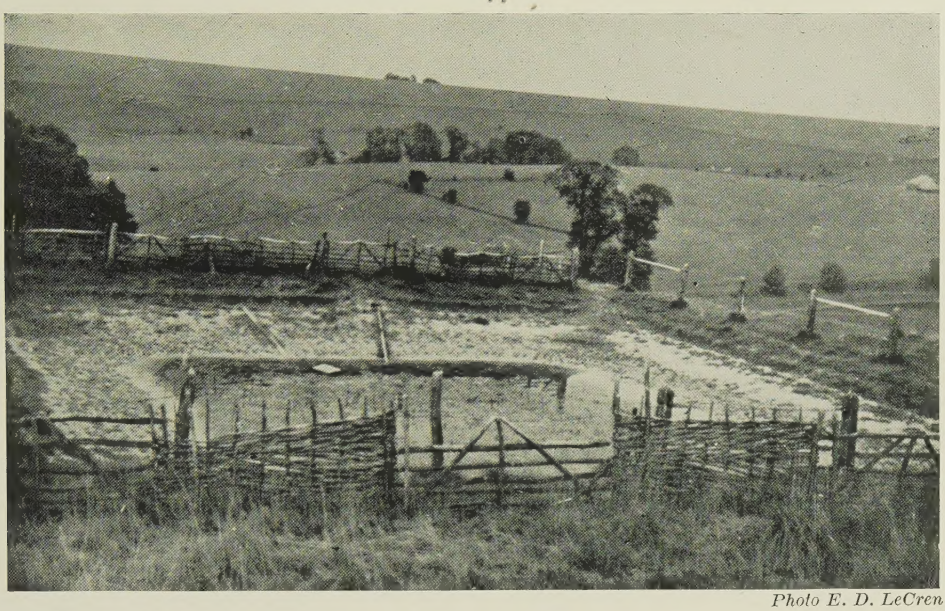

Photo E. D. LeCren

Photo 1. Pond D 2. A typical fenced, uncleaned dewpond.

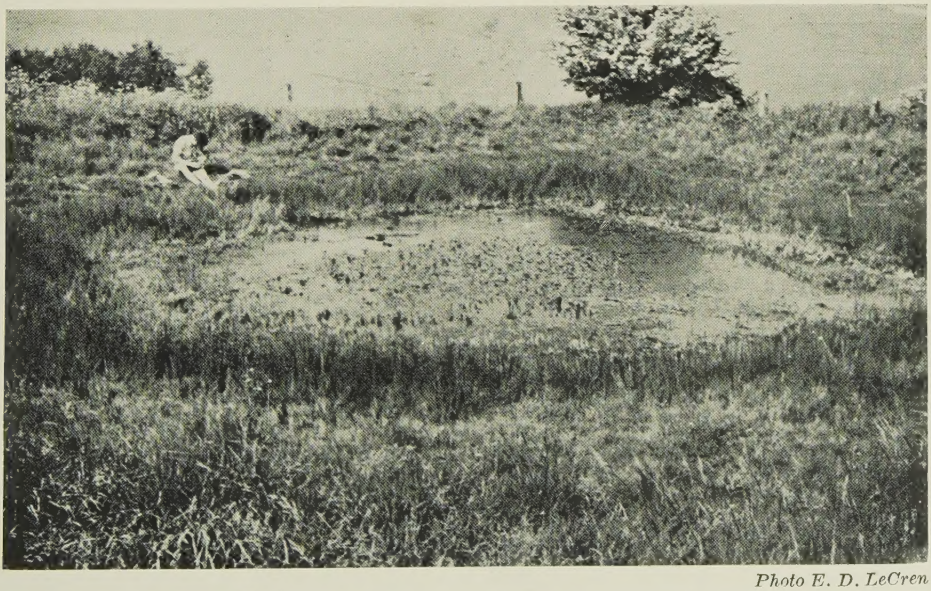

Photo E. D. LeCren

Photo 2. Pond D 4. A long disused dewpond with much vegetation.

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siderably. Martin's results appear to have all been taken during August 1909, which he states had suffered an exceptionally dry summer. It is interesting to note that the two sets of figures agree in indicating large quantities of sodium carbonate in the very foul 'green' ponds.

Pond	Date	Tem-porary hardness	Sodium car-bonate	Total hardness	Turbidity
D 23	11 Feb. 1941	121	67	—	Fairly clear
D 23	13 June 1941	130	260	—	Very turbid
D 24	11 Feb. 1941	111	30	—	Clear
D 24	13 June 1941	136	47	—	Fairly clear
Lowest figures given by Martin	—	8·5	—	61	Clear
Three highest figures from Martin	16 Aug. 1909	—	130	163	Very turbid and green
	16 Aug. 1909	—	37	166	Very turbid
	—	231	—	302	Very foul

— Means that no figures are available.

3. Location of the ponds visited

During 1939 and 1940 Macfadyen investigated 31 dewponds in the neighbourhood of Dauntsey's School near Devizes, Wiltshire; a number of these ponds have been visited several times and some have been studied intensively by members of the Dauntsey's School natural history society. In 1940 Macfadyen collected in 44 ponds between Marlborough and Devizes, Wiltshire, and in 6 ponds near Alfriston in Sussex. Of these 81 ponds, 45 hold water for the greater part of the year or throughout the year and nearly all the 45 harbour water bugs. In addition there are records from 4 ponds between Pertwood Down and Little Down alongside the Warminster to Shaftesbury road (A 350) visited by Macan, and from one pond studied by Messrs Banks and Moon who have kindly supplied information. Water bugs were found in all these ponds and the total number considered in the following pages is thus 50. Of these 16 were 'true' dewponds, according to the nomenclature of Pugsley (1939), that is, they received no surface drainage; and 31 were 'assisted' dewponds. Three (B 15, B 31 and B 40) were not dewponds in the strict sense, but they have been included as they did not appear to differ greatly from dewponds in ecological features, and aquatic habitats other than dewponds are rare on the chalk downs.

Detailed maps showing the position of each dewpond are deposited with the Freshwater Biological Association at Wray Castle, Ambleside.

4. Technical details

The collections were made with a hand-net. Macfadyen aimed at getting 50–100 specimens of *Sigara* from each pond; when they were scarce he went on fishing for 20 or 30 min. The results of collections which did not

conform to this standard are omitted from Table 1, but included in the totals below. Less care was devoted to the collection of other water bugs. For each pond notes were made on the fluctuation of water level, the extent of pollution by beasts, the transparency of the water, the source of water supply, the nature of the bottom, the vegetation and the fauna. The results of these observations are summarized in Table 1. Plants included in the column headed 'Total number of plants', but not listed specifically, were *Carex*, *Juncus* and *Ceratophyllum* each in two ponds, and *Elodea*, *Glyceria* and *Potamogeton crispus* each in one pond. *p*H was measured in the field by means of B.D.H. universal indicator. Corixidae are named according to the check list of China (1938).

5. The water bug fauna

The following is a complete list of the Heteroptera taken, the numbers being based on every collection made.

	No. of specimens	No. of ponds
Sigara lateralis (Leach) (hieroglyphica Duf.)	1050	33
S. nigrolineata (Fieb.) (fabricii Fieb.)	224	31
Corixa punctata Illig (geoffroyi Leach)	143	27
Sigara limitata (Fieb.)	56	11
S. sahlbergi (Fieb.)	9	5
S. distincta (Fieb.)	5	4
S. striata (Linn.)	4	3
S. falleni (Fieb.)	3	3
S. praeusta (Fieb.)	3	3
Corixa panzeri Fieb.	6	2
Sigara germari (Fieb.)	3	2
S. moesta (Fieb.)	6	1
S. castanea (Thoms.)?	1	1
S. concinna (Fieb.)	1	1
Notonecta maculata Fab.	61	14
N. o. obliqua Gall. (furcata Fab.)	41	17
N. obliqua delcourti Poisson	28	10
N. g. glauca Linn.	10	8
N. v. viridis Delc. (halophila Edw.)	9	1
Plea leachi McGreg. & Kirk. (minutissima Fab.)	8	1
Gerris lacustris (Linn.)	19	?
G. thoracicus Schum.	16	?
G. odontogaster Zett.	4	?
Naucoris cimicoides (Linn.)	6	1
Ranatra linearis (Linn.)	From D 24, a pond which has received a good deal more attention than any of the others	
Nepa cinerea Linn.		

Further details of the occurrence of the commoner species are presented in Table 1, which includes all the ponds which held water for the greater part of the year. It will be seen that there is considerable disparity in the number of

Table 1. *Ecological features and principal water bugs of dewponds*

Degree of pollution:
A much or very much.
B fair or intermediate.
C slight or none.

Transparency of water:
A clear or very clear.
B slightly milky or clear but tinted.
C thick or very thick.

Degree of permanence:
A water level subject to slight or moderate fluctuation.
B water level subject to considerable fluctuation.
C pond dries up in times of drought.

Pond number	Vegetation: *Ranunculus aquatilis*	*Lemna*	*Chara*	*Potamogeton natans*	*Myriophyllum*	*Sparganium*	*Scirpus*	*Equisetum*	*Rumex*	Total number of plants	Nature of bottom	pH	Degree of pollution	Transparency of water	Degree of permanence	Surface drainage from land	Corixidae: *Corixa punctata*	*Sigara lateralis*	*S. nigrolineata*	*S. limitata*	Notonectidae: *Notonecta obliqua obliqua*	*N. o. delcourti*	*N. glauca glauca*	*N. maculata*	*N. viridis viridis*	Date of collection	Other fauna: *Eristalis*	Chironomids	Odonata	*Cloëon*	*Limnaea peregra* (Müller)	*L. stagnalis*	Smooth newt (*Triturus vulgaris*)	Crested newt (*T. palustris*)	Remarks
B 19	.	.	.	.	.	.	.	.	.	0	Chalk and dung	10·0	A	C	A	–	.	66	.	.	.	.	.	.	31 July 1940	.	×	.	.	.	.	.	.	
B 18	.	.	.	.	.	.	.	.	.	0	Chalk and dung	10·0	A	C	A	+	.	92	.	.	.	.	.	.	31 July 1940	.	.	.	.	.	.	.	.	
B 16	.	.	.	.	.	.	.	.	.	0	Chalk and dung	10·0	A	C	A	+	4	144	.	.	.	.	.	.	30 July 1940	.	×	.	.	.	.	.	.	
D 31	.	.	.	.	.	.	.	.	.	0	Chalk and dung	9·0	A	C	A	–	2	29	5	.	.	.	.	.	29 July 1940	.	×	.	.	.	.	.	.	
D 20	.	.	.	.	.	.	.	.	.	0	Chalk and dung	8·25	A	C	A	+	6	118	.	.	.	.	.	.	21 May 1940	×	.	.	.	.	.	.	.	
																		41	2						14 July 1940	.	.	.	.	.	.	.	.	
M 1	.	.	.	.	.	.	.	.	.	0	Chalk and dung	.	A	C	A	+	.	14	.	.	.	.	.	.	23 Apr. 1939	.	×	.	.	.	.	.	.	
BM	.	.	.	.	.	.	.	.	.	0	Chalk and dung	.	A	C	A	+	.	Many	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
B 8	×	.	.	.	.	.	.	.	.	1	Chalk and dung	9·5	A	C	A	+	.	58	9	.	.	.	.	.	29 July 1940	.	.	.	.	.	.	.	.	
B 17	.	.	.	×	.	.	×	.	.	2	Chalk, dung and humus	8·0	A	C	A	+	11	44	.	.	.	8	.	1	31 July 1940	.	×	.	×	.	.	.	.	
B 34	.	.	.	×	.	.	.	.	.	2	Chalk lumps	9·0	A	C	A	+	.	26	2	.	.	2	1	.	1 Aug. 1940	.	×	.	×	.	.	.	.	
D 23	.	.	.	×	.	×	.	.	×	3	Chalk and dung	8·25	A	C	A	+	7	12	.	.	.	.	.	.	6 July 1939	.	×	.	.	×	.	.	.	
																		44	2						4 June 1940	.	.	.	.	.	.	.	.	
A 1	.	.	.	.	.	.	.	.	.	0	Concrete with chalk	8·5	C	B	A	+	.	.	.	.	.	.	.	.	21 Mar. 1940	.	.	.	.	.	.	×	×	Pond new
A 5	.	.	.	.	.	.	.	.	.	0	Humus	8·5	C	C	A	–	.	.	.	.	.	.	.	.	21 Mar. 1940	.	.	.	.	.	.	×	×	Much filamentous alga and grass
B 29	.	×	.	×	.	.	.	.	.	3	Humus	8·0	C	B	A	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.		
B 1	.	×	.	.	.	.	×	.	.	2	Humus	8·0	C	B	A	+	.	.	.	.	1	.	.	1	29 July 1940	.	.	×	.	×	.	×	×	
B 13	.	×	.	×	.	.	.	.	.	2	Humus	7·5	C	B	A	–	.	.	.	.	3	.	1	1	30 July 1940	.	×	×	.	×	.	.	.	
A 2	×	.	×	.	.	.	.	.	.	2	Concrete and humus	8·5	C	B	A	+	Common	.	.	.	.	.	.	.	21 Mar. 1940	.	.	.	.	×	.	.	.	
B 40	×	×	.	.	.	.	.	.	.	2	Humus	8·0	B	B	C	+	7	.	.	.	.	.	.	.	2 Aug. 1940	.	.	.	.	.	.	×	.	
D 22	×	.	.	.	.	.	×	.	×	3	Chalk and humus	8·25	C	A	C	+	3	.	.	.	3	.	.	1	6 July 1939	.	.	×	.	.	.	×	.	
D 6	×	×	.	×	×	.	×	.	.	5	Chalk and humus	8·0	C	A	A	+	4	.	.	.	2	.	.	.	6 July 1939	.	.	×	×	.	×	.	.	
D 4	.	.	×	×	×	×	×	.	.	5	Humus	8·0	C	B	A	+	1	.	.	.	4	.	.	.	28 July 1940	.	.	×	×	.	×	.	.	
D 7	×	×	×	.	.	.	.	.	×	4	Chalk and humus	8·5	C	A	A	–	.	.	.	.	2	2	.	.	28 July 1940	.	.	.	.	.	×	.	.	
B 42	.	×	×	×	.	.	.	.	.	5	Humus	.	C	B	A	–	1	.	.	.	.	.	2	.	2 Aug. 1940	.	×	.	.	.	.	×	×	
B 37	.	.	×	.	.	.	.	.	.	1	Chalk lumps	9·5	C	B	A	–	4	.	.	2	2	.	1	5	9	.	.	×	.	×	.	.	.	Cleaned occasionally
B 24	.	.	.	×	.	.	.	.	.	2	Humus	7·0	C	B	A	–	1	.	.	1	2	3	.	.	31 July 1940	.	.	.	×	.	×	×	.	
D 16	.	×	.	×	.	×	×	.	.	5	Chalk and humus	8·0	C	B	A	+	1	.	3	.	2	1	1	2	29 July 1940	.	.	.	×	.	×	×	.	
D 1	×	.	.	×	.	.	.	.	×	3	Chalk and stone	9·0	C	B	B	+	1	.	1	.	1	.	.	.	28 July 1940	.	.	×	×	×	.	×	.	
B 36	.	×	.	.	.	.	.	.	.	1	Chalk and humus	7·5	B	B	A	+	10	5	1	1	1	1	.	.	2 July 1940	.	×	×	.	.	.	.	.	
B 9	.	.	×	.	.	.	.	.	.	1	Chalk lumps	8·0	C	B	A	–	17	17	.	2	.	.	.	1	30 July 1940	.	×	.	×	×	.	×	.	
B 22	.	.	.	.	.	.	.	.	.	0	Flint and humus	7·5	C	C	A	–	25	22	2	2	1	.	.	.	31 July 1940	.	×	.	.	.	×	.	.	Branches in water
D 26	×	×	.	.	.	.	×	.	.	4	Chalk, dung and humus	8·5	B	C	B	+	6	.	3	4	1	.	.	.	6 July 1939	.	×	.	.	×	.	×	.	
																		1	9						28 July 1940									
D 24	.	.	.	×	.	×	×	.	.	3	Chalk, dung and humus	.	B	B	C	+	6	7	3	1	.	.	.	.	6 July 1939	.	.	.	.	×	.	×	×	
																					3	.	2	3	29 July 1940									
D 8	.	×	.	×	.	.	.	.	.	2	Humus	8·5	C	B	A	+	13	27	4	2	4	2	1	.	28 July 1940	.	.	.	×	.	.	×	.	
B 35	.	.	×	.	.	.	.	.	.	1	Chalk	9·0	C	B	B	+	3	17	3	22	.	.	1	6	2 Aug. 1940	.	×	.	.	×	.	×	×	Cleaned annually
D 2	.	.	×	×	×	×	×	.	×	6	Chalk	9·0	C	B	A	+	2	20	27	4	.	.	.	.	17 Feb. 1940									
																	1	21	20	7	1				3 Mar. 1940	.	.	×	.	×	.	×	.	
																	1	.	3	2	1	2	.	7	28 July 1940									
D 5	×	.	.	×	×	.	×	.	×	6	Chalk and stone	8·5	B	B	B	–	.	.	6	4	2	.	.	.	28 July 1940	.	.	×	×	×	.	×	.	
A 6	.	.	.	.	.	.	.	.	.	0	Concrete and humus	10·0	C	B	A	–	.	56	5	13	.	.	.	.	22 Mar. 1940	.	.	.	.	.	.	.	.	
D 14	.	×	×	×	.	.	.	.	.	3	Concrete and humus	8·3	C	B	A	+	3	1	4	.	.	.	.	.	27 May 1940	.	×	×	.	×	.	×	.	
M 4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	1	4	.	.	.	.	.	23 Apr. 1939	.	.	.	×	.	×	.	.	
B 23	.	.	.	×	.	.	.	.	×	2	Concrete and humus	7·5	C	B	A	–	.	3	2	2	2	4	.	.	31 July 1940	.	.	.	×	.	×	×	.	
B 10	.	.	.	.	.	.	.	.	.	0	Concrete and chalk	9·5	C	B	C	–	.	71	8	.	.	.	.	.	30 July 1940	.	×	.	.	.	.	.	.	Dry about a week previously
B 20	×	.	.	.	.	.	.	.	.	1	Chalk and humus	9·0	C	B	C	–	1	34	20	.	.	.	.	.	31 July 1940	.	.	.	.	.	×	.	.	
B 28	.	.	.	.	.	.	.	.	.	0	Chalk	8·0	B	B	C	–	.	3	1	.	.	.	.	.	1 Aug. 1940	.	×	.	.	.	.	.	.	
B 26	.	.	.	×	.	.	.	.	.	1	Concrete and humus	8·0	B	B	A	+	.	5	6	.	4	3	.	.	31 July 1940	.	.	×	×	.	×	×	.	
M 3	.	.	×	×	.	.	.	.	.	2	Black mud	.	C	.	.	+	.	3	2	.	.	.	.	.	23 Apr. 1939	.	.	.	.	.	×	.	.	
D 25	.	.	.	.	.	.	.	.	.	0	Concrete, dung and humus	8·0	B	B	A	+	.	6	19	.	.	.	.	.	29 July 1940	×	×	.	×	.	×	.	.	Bed of *Scirpus* washed out by flood in Jan. 1940
B 31	.	.	.	.	.	.	.	.	.	0	Concrete	8·5	C	A	C	+	.	1	16	.	.	.	.	.	1 Aug. 1940	.	.	×	.	.	.	.	.	Concrete tank
M 2	.	.	×	×	.	.	.	.	.	2	Chalk	.	C	.	.	+	.	.	12	.	.	.	.	.	11 June 1936	.	.	×	.	.	×	×	.	
B 12	.	.	.	×	.	×	.	×	.	3	Chalk and humus	7·0	C	B	B	+	.	.	10	.	.	.	.	.	30 July 1940	.	×	.	.	.	.	×	.	
B 15	.	.	.	.	.	.	.	.	.	0	Chalk and humus	7·5	C	A	A	–	.	.	7	.	.	.	.	20	30 July 1940	.	×	.	.	.	.	.	.	2 iron drinking troughs

specimens captured in different ponds, and this is clearly a point which calls for examination. Big populations are found in all the highly polluted ponds. In the remainder the density of population tends to decrease as the density of vegetation increases. Roughly the density of vegetation is proportional to the number of species present and the point is brought out in the following table:

No. of plant spp.	No. of ponds	No. with less than 10 Corixids	No. with 10–20 Corixids	No. with over 20 Corixids	No. with *Notonecta*
0	8	4	1	3	2
1	9	2	2	5	6
2	7	5	1	1	3
3	7	5	2	0	4
4	2	2	0	0	2
5	5	4	1	0	3
6	2	0	1	1	2

Of the four ponds with no vegetation and less than 10 Corixids, A 1 was new, B 28 was nearly dry, A 5 was overgrown with grass and filamentous algae and B 15 was a pair of small iron drinking troughs. It seems likely that thick vegetation produces humus which makes the pond less suitable for Corixids, and in this connexion it is noteworthy that D 2, the only pond with much vegetation and a good Corixid population is the only pond with little fluctuation of water level which has more than two species of plant but no humus on the bottom. However, there appears to be some relation between *Corixa punctata* and humus and there is evidence that in different ponds there are different soil conditions, which, perhaps, could only be detected by chemical analysis.

Only a few of the ponds have been visited on more than one occasion. The limited data obtained from these indicate that the population may change rather violently both in composition and numbers in a comparatively short time. Chance is, therefore, a factor which may be important in the ecology of water bugs in dewponds, and this must be borne in mind when the occurrence of individual species is being considered.

Abundance of *Sigara lateralis* is correlated with considerable pollution, for this species was numerous in each of the 11 ponds which were highly polluted, but it is not confined to such ponds. It occurs in temporary ponds and in permanent ponds. It evidently colonizes the former rapidly, for 71 specimens were found in B 10 which had been dry a week previously, confirming the observation of Macan (1939) that this species flies readily. It is found in ponds with no vegetation and ponds with much vegetation, though in the latter it tends to inhabit open patches free of plant growth. *S. lateralis* is present and usually abundant in all the ponds which provide a favourable environment for Corixids: thus, it is numerous in all the 7 ponds where the numbers of any other species exceed 16. Both *Corixa punctata* and *Sigara nigrolineata* are closely associated with it, that is they occur together in many ponds and are often abundant in the same pond. *C. punctata* and *S. nigrolineata* themselves are,

however, not closely associated and the two are never abundant in the same pond. It seems, therefore, that, from generally good conditions, ponds develop in two directions, one direction leading to conditions which only *C. punctata* can tolerate, the other to conditions which only *S. nigrolineata* can tolerate. This is shown in Fig. 1.

Corixa punctata is less common than *Sigara lateralis*, in that it occurs in fewer ponds and is much less abundant, though the figures in Table 1 do

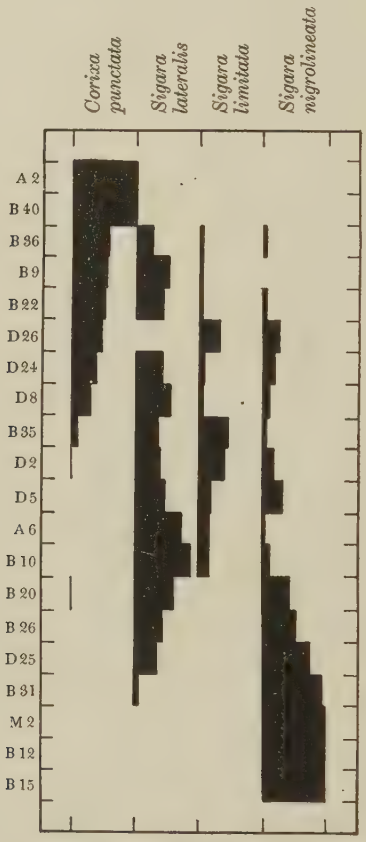

Fig. 1. Proportions of the four common species of Corixid in dewponds. The histogram does not include (*a*) ponds where the numbers of the commonest species was less than six, (*b*) highly polluted ponds.

not give an entirely satisfactory indication of its relative abundance, as it was not always collected as carefully as the species of *Sigara*. *C. punctata* is associated with conditions favouring the development of *Lemna* for it is present in every *Lemna*-covered pond harbouring Corixids; and in B 40, which is completely overgrown, it is the only species present. This line of development leads to conditions where only *Notonecta* is found (B 1, B 13) and eventually to conditions where there are no bugs at all (B 29). All the *Lemna*-covered ponds

have a relatively low *p*H (7·5–8·5). *C. punctata* is also found in 8 out of the 11 ponds containing *Chara*. Unlike the other common species, *C. punctata* is rare in ponds with no vegetation. It is only recorded from 4 of them; in one (B 22) it is abundant, but in this pond there are branches in the water. It is also less abundant in temporary ponds than the other common species.

Sigara nigrolineata is as common as but much less abundant than *S. lateralis*. It is rare in ponds in which conditions are suitable for *C. punctata*, but it is difficult to draw any positive conclusions about its ecological requirements. It appears to be indifferent to the presence or absence of vegetation, but it tends to occur more commonly in temporary and small ponds. Two of the ponds in which *S. nigrolineata* is the only or almost the only species present do not properly belong to the present survey at all. B 31 is a concrete tank filled with well water by a wind pump and B 15 is a pair of small iron drinking troughs.

Sigara limitata is closely associated with *S. lateralis*, though it is usually found where there is some vegetation, and only a single specimen has been found in all the highly polluted ponds. Although only 9 specimens of *Sigara sahlbergi* from 5 ponds were taken, it is noteworthy that all the ponds had both *Lemna* and *C. punctata*. All were long disused, heavily vegetated and had grass growing right down to the water's edge.

Notonecta occurs in half the total number of ponds. It is found chiefly in the more permanent ponds and in the ponds which have some vegetation. It is more common in the ponds harbouring *Corixa punctata* and *Lemna* and *Notonecta g. glauca* is only found in these.

In view of the number of ponds visited, the area covered and the fact that the important species are not confined to a small number of ponds, it seems justifiable to treat the dewpond as an ecological unit. It is characterized by complete isolation, calcareous water and in some cases by pollution, and the comparison of its fauna with that of localities where other characters are predominant should yield information about the relation of these characters to the ecology of Corixidae. 'True' dewponds offer an extreme instance of isolation, for not only is there no inflow or outflow, but the water is not in contact with a general water table. As Corixidae appear to fly readily (Macan, 1939), the existence of a land barrier is not likely to affect their distribution greatly, and the significance of isolation from the ecological point of view lies more probably in its effect on the chemical nature of the mud and the water. The importance of this factor in Corixid ecology is revealed when the dewpond fauna is compared with that of some locality which is calcareous but not isolated. A good example of such a locality is Wicken Fen, where the aquatic habitats are slowly flowing ditches, or pools which are affected by a general movement of the water table and which are in communication with the rest of the fen in times of flood. Hutchinson (1925) records *Sigara sahlbergi*, *S. linnei*, *S. striata*, *S. falleni*, *S. fossarum* and *Cymatia coleoptrata* as the

common species; *S. lateralis* and *S. limitata* are not recorded at all. It is also noteworthy that *S. striata* and *S. falleni* are the common species inhabiting the rivers which flow off the chalk downs.

Comparisons with non-calcareous districts such as the Lake District or South Haven Peninsula, Dorset, illustrate the ecological significance of calcium. In the Lake District there are many localities which resemble dewponds in being small and isolated, but all the waters are deficient in lime. With the exception of *S. nigrolineata*, all the Corixids important in dewponds are rare and scarce in the Lake District (Macan, 1938); *S. nigrolineata* is abundant at high altitudes in association with typical northern species such as *S. wollastoni* and *S. carinata*, a distribution which suggests that a biological race may be involved. At South Haven Peninsula, a non-calcareous district closer at hand to the dewponds studied, none of the important dewpond species are common or abundant.

The correlation between *S. lateralis* and pollution is confirmed by the following collection from six ponds used for the final purification of the sewage from Welwyn Garden City, Hertfordshire:

S. lateralis	113	S. distincta	1
S. concinna	12	S. nigrolineata	1
S. striata	12	C. punctata	1
S. praeusta	10	Notonecta glauca glauca	2
		N. viridis viridis	1

6. Summary

1. The general features of dewponds are summarized and water bugs from 50 collections in Wiltshire and Sussex are tabulated.

2. Fourteen species of Corixidae have been found, but only 4, *Sigara lateralis*, *S. nigrolineata*, *Corixa punctata* and *S. limitata*, are common and abundant; all five British species and varieties of *Notonecta* and a few other water bugs are recorded.

3. Large numbers of Corixidae are found in all the ponds highly polluted by sheep and cattle; in other ponds the number of bugs present tends to decrease as the density of vegetation increases.

4. *Sigara lateralis* is abundant in all the ponds much polluted by sheep and cattle. It is also numerous in some other ponds, particularly those which appear to be suitable for Corixids generally. *Corixa punctata* is associated with conditions which lead to the formation of a foul mud and the presence of *Lemna*; it is seldom found in the less permanent ponds or in those where there is no vegetation. *Sigara nigrolineata* is never numerous under conditions which favour abundance of *C. punctata*; it is often found in the smaller, less permanent ponds. *S. limitata* is closely associated with *S. lateralis*, but it is rare in polluted ponds.

5. *Notonecta* is found chiefly in the more permanent ponds, particularly those where there is some vegetation.

6. Dewponds are characterized by isolation and by calcareous water and some of them are highly polluted. The dewpond fauna is compared with that of localities where these characters are not found and the importance of these factors in the ecology of Corixidae is discussed.

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CANADIAN ARCTIC WILD LIFE ENQUIRY, 1939–40[1]

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(*With Plate 3 and 5 Figures in the Text*)

1. Introduction

This is the fifth annual summary of information about certain animals in the Canadian Arctic and Subarctic. Answers to 37 questionnaires, received by the Northwest Territories Administration, Ottawa, were forwarded for analysis to the Bureau of Animal Population (22 were relevant to wild life), and 63 of the annual zoological reports from posts of the Hudson's Bay Company included similar data on lemmings (*Lemmus* and *Dicrostonyx*), arctic fox (*Alopex lagopus*) and snowy owl (*Nyctea nyctea*). Reports on the health of sledge dogs are also included from many other observers besides these 85.

From the reports of change in lemmings, foxes and owls the general course of events has been followed from 1935 to 1940, each year ending 31 May being compared with the one before. To discuss the history of each individual post is beyond the scope of this paper, though the data are available to anyone who is interested in exceptions to the general conclusions presented below. It is considered best at this stage to discuss the posts in the geographical groups by which the reports are summarized in Table 2 in each of the five papers. These tables show the number of opinions of each kind, and for groups 1, 2, 6 and 8 the figures have been used without corrections. Reports have been omitted from Devon and Ellesmere Islands (group 7) and from group 4 when they do not refer to conditions on the coast (see last report, p. 232). As an example, there were in 1939–40 in group 1, Northern Labrador coast, nine reports about arctic fox, all of which were *decrease*. The previous year there were 11 reports: *increase* 6; *decrease* 4; *no change* 1. The two years may therefore be compared by saying that reports of increase fell from 55 % in 1938–39 to zero in 1939–40. Fig. 5 shows in what proportion each type of reply was given; but it should be realized that the diagrams are based on very small numbers of reports and are therefore useful only as rough guides to the written descriptions. Naturally these diagrams do not show population growth, which, for instance, in the second year of general increase would show a rising and not a level curve.

2. Results

Northern Labrador Coast (group 1). In the first year of this study (1935–36) lemmings, 'mice', foxes and owls were almost everywhere reported as much scarcer than in the previous year. Reports about 'mice' are not summarized;

[1] Promoted by the Northwest Territories Administration of the Canadian Government, Ottawa.

but in this group particularly there is unlikely to have been any clear distinction between small rodent species, chief of which is probably the Labrador vole *Microtus enixus* (Anderson, 1934). During 1936–37 all species showed a slight local improvement which became well marked a year later and 'mice' and lemmings evidently grew very abundant. In most places they continued to increase for another year, but by 1939–40 no centres of abundance were left. Foxes and owls also continued to increase in some places early in 1938–39 but had decreased everywhere by the following year.

Nutak. 'White fox were very scarce, and the inland hunters again found very little "sign" during their winter and spring trips.'

Northern Quebec and Baffin Island (groups 2, 6 and 7 except Devon and Ellesmere Islands). Increase in all species was reported up to 1937–38 and many people had expected white fox to continue on to a peak during 1938–39. In this all were disappointed and a poor season occurred just three years after the previous low. The latest reports, unlike those from Northern Labrador, indicate a good recovery of lemmings and snowy owls during 1939–40; and unlike 1936–37 (the first year of recovery after the previous general decrease) foxes have been reported on the increase at fewer posts. It will be interesting to see if this means that a peak will be reached less abruptly.

Payne Bay. 'This past spring foxes seem to be more plentiful and are migrating from inland towards the coast. Lemming and wild mice, the natural food of the foxes, are in abundance. The white owl, which is looked upon as the harbinger of the foxes, seems to be abundant.'

Diana Bay. 'Lemming have been exceptionally abundant all spring, travelling on the sea ice in large numbers heading towards the running ice. The snowy owls have been exceptionally abundant all winter. In June [? 1940] the lands around the post and all ground covered by natives were overrun by lemmings. The white fox catch was not what it should have been according to the signs, for the foxes would not go to the bait at all this winter.'

Payne Bay, Diana Bay and Leaf River were exceptional in passing their last peak of fox abundance some months before the other posts in these groups.

Sugluk West. 'Late in the month of May the natives reported having seen lemming tracks all over the countryside. Locally there are not many lemmings, but snowy owls and duck hawks were much in evidence, so this fact in itself, would corroborate the native report.'

Povungnetuk. 'Lemmings were very plentiful inland after last week of May 1940, also several varieties of hawks preying on them. Foxes definitely increased inland in late May 1940.'

Pond Inlet. 'It was only in the spring of 1940 that lemming became exceptionally abundant. In the summer and fall of 1939 they appeared to be scarce, but after the return of "daylight" in February, signs were plentiful.'

Southampton Island, Repulse Bay and Chesterfield Inlet (group 5 and northern coastal parts of 4). Lemmings at these three posts seem to have been in quite a different phase of abundance from that on Baffin Island or the Quebec-Labrador mainland, having reached a peak as early as 1935–36, become scarce

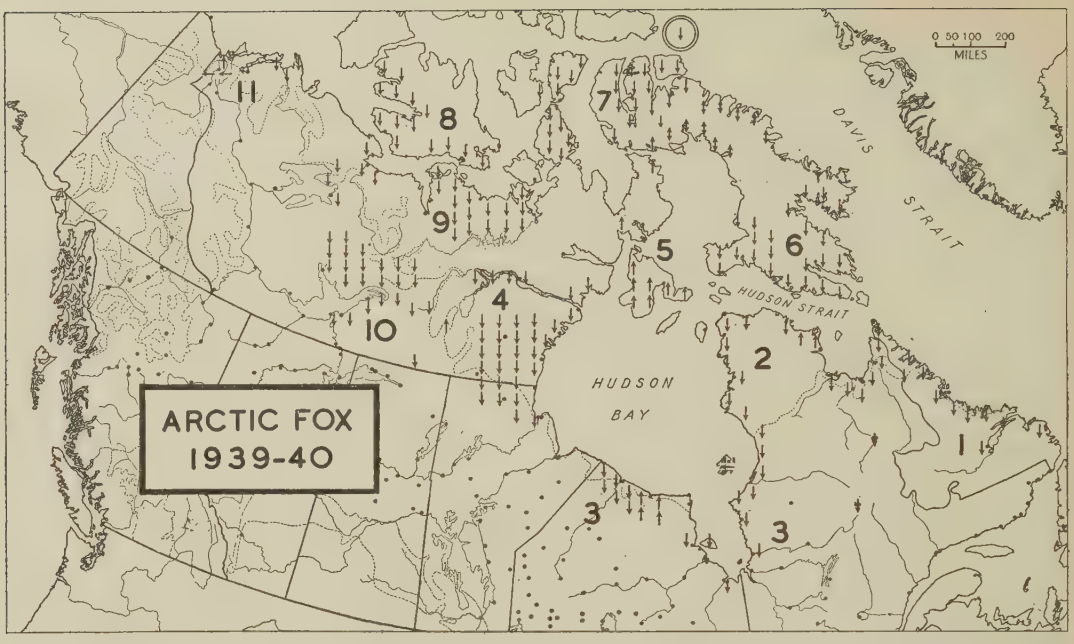


Fig. 1. State of the arctic fox population in 1939–40 compared with 1938–39. Arrows show the areas covered by observers reporting INCREASE (↑), DECREASE (↓), and NO CHANGE, NOT ABUNDANT (←). Small black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset: Craig Harbour, Ellesmere Island.

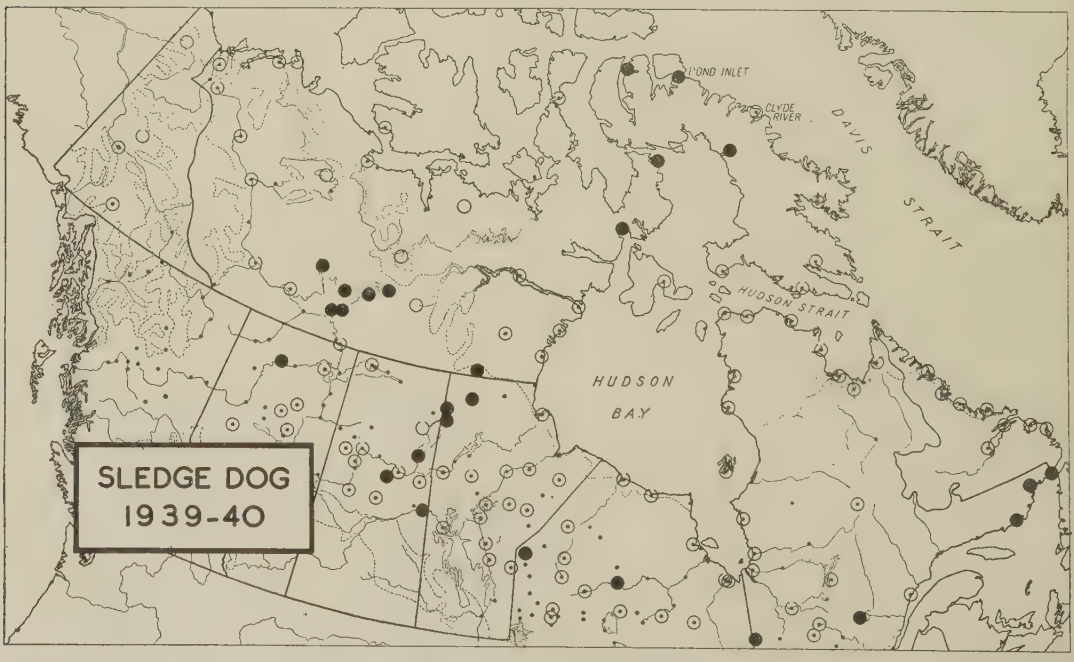


Fig. 2. Prevalence of disease among sledge dogs in 1939–40. Reports of serious disease are shown ●; disease entirely absent: ○; other reports: broken circle. Small black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones.

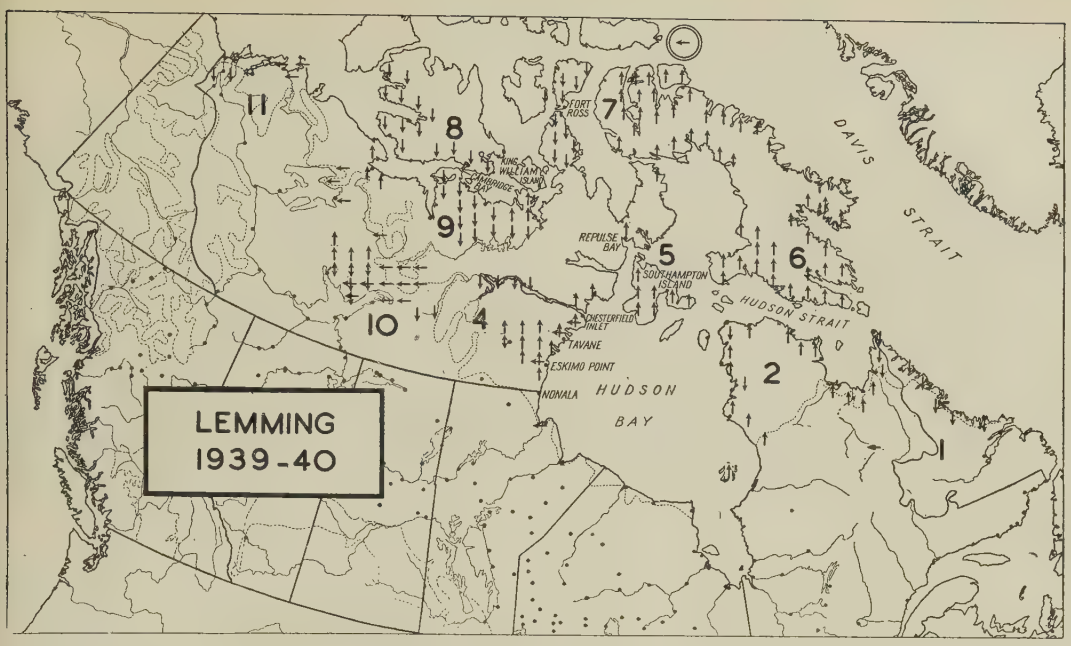
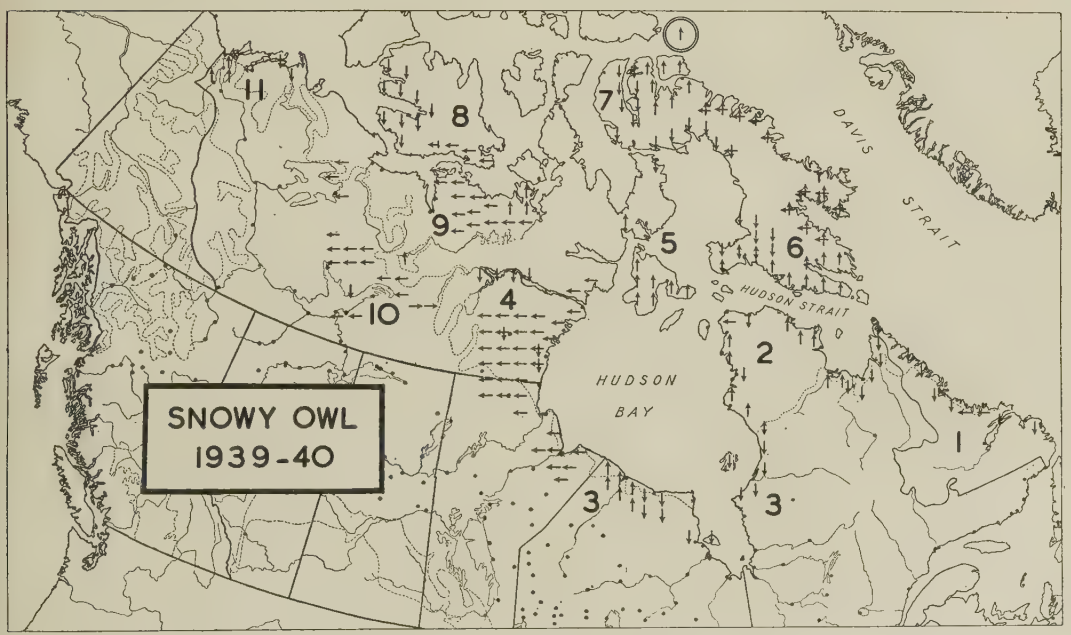


Fig. 3.



Figs. 3, 4. State of the lemming and snowy owl populations in 1939–40 compared with 1938–39. Arrows show the areas covered by observers reporting INCREASE (↑), DECREASE (↓), NO CHANGE, NOT ABUNDANT (←), and NO CHANGE, ABUNDANT (→). Small black dots are Hudson's Bay Company posts. Broken lines show main vegetation zones. Inset: Craig Harbour, Ellesmere Island.

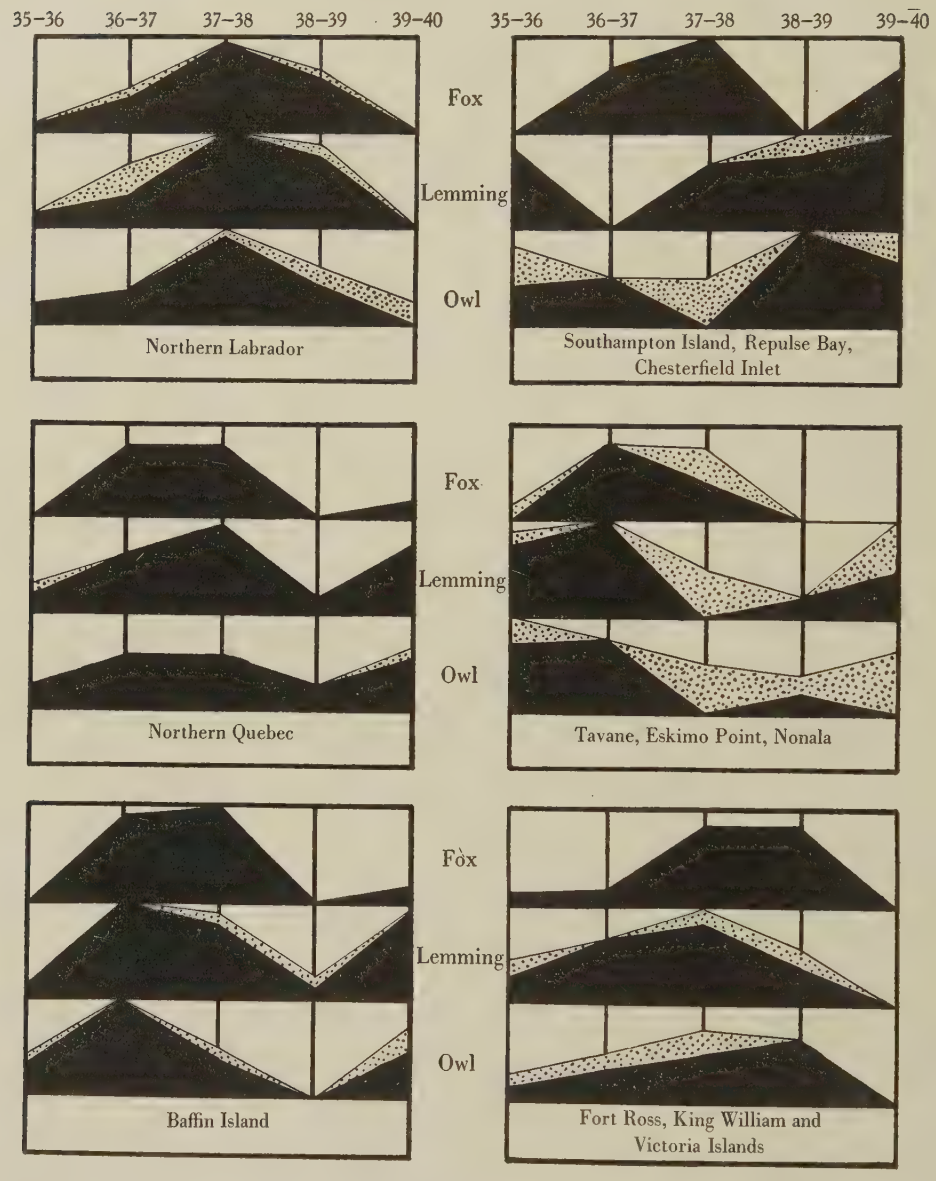


Fig. 5. Proportion of reports stating INCREASE (black), DECREASE (white) and NO CHANGE (stippled) in each year 1935–40 for different parts of the Arctic. Figures from Tables 1 and 2 in each year's paper.

and since recovered. At Chesterfield Inlet this difference was quite apparent on 10 August 1939 when two members of the Eastern Arctic Patrol (L. L. Lyster and D. Chitty) captured several *Lemmus trimucronatus* by hand from under stones near the settlement. At most other ports of call of the R.M.S. *Nascopie*, the Hudson's Bay Company supply ship for the Eastern Arctic (Anderson, 1939), a search was made for lemmings without finding signs except of past abundance. At Port Burwell, for example, old droppings were exceedingly plentiful in crevices among the hills but no fresh traces were found in a two hour search. Information about 1939–40 is as follows:

Southampton Island. 'Fox migration to Island took place in April and March 1940, mainly from the east, but also, to a lesser degree, from the west and south-west. Lemming not particularly abundant during fall months but increased rapidly during the winter, January to March especially.'

Repulse Bay. 'White fox tracks fairly numerous all winter but would not take bait on traps due no doubt to large number of lemming and mice around.'

Chesterfield Inlet. 'Lemming abundant. White fox scarcer and refusing to take bait.'

Arctic fox, despite the earlier start of recovery in lemmings, was not reported to be following a correspondingly different trend. Thus in 1938–39 decrease was reported at the three posts, as elsewhere in the Eastern Arctic, although this was the second year of increase in lemmings, at least at Southampton Island and Repulse Bay.

Snowy owls started to increase in 1938–39 and maintained or improved their numbers the year following.

Tavane, Eskimo Point, Nonala (group 4, southern coastal posts). 'Mice' and lemming have here shown yet another phase of population density, for in 1937–38 when most other observers noted increase or abundance, here decrease and scarcity had set in. There has since been some recovery and large numbers were seen in the spring of 1940:

Tavane. 'During April and early May exceptional migration of lemming observed and reported by various sources from Eskimo Point to Chesterfield Inlet. These animals were apparently travelling eastwards and large numbers (several thousands at least) were seen perished on the salt water ice.'

Eskimo Point. 'Lemming and mice were particularly abundant in May and June 1940. They were abundant in the fall of 1939 but not remarkably so. White fox was very scarce both winter and spring although abundant in early fall locally. All foxes in very good condition with no sign of lack of country food.'

Snowy owls apparently passed their peak with the lemmings and there has also been less increase in foxes reported since then.

Fort Ross, King William and Victoria Islands (group 8). Lemmings on the west coast of Victoria Island reached a peak during 1938–39 and a description (quoted in that year's report) was given from Read Island of the disappearance of large numbers by spring 1939. However, in 1939–40 further evidence of abundance was seen. At Cambridge Bay, south-east Victoria Island, and in the King William Island and Fort Ross areas it is possible that the peak

was passed a year earlier; and though the evidence about this is not very satisfactory, the start of increase was certainly reported one year earlier at Cambridge Bay and King William Island than on the west coast. Arctic fox apparently increased through 1938–39 not only on the west coast but at Cambridge Bay and Fort Ross. After this, decrease occurred everywhere in all three species.

Read Island. 'Some natives reported this spring coming across considerable numbers of dead bodies of lemming on the ice between here and Williams Point, but they could not tell from which direction they had come.'

Holman Island. 'During the months of October and early November lemming and white fox started an easterly migration and by the end of November their numbers had diminished. As soon as the Prince of Wales Straits had frozen over, there was a "run" from Banks Island eastward. During the month of June reports have come in from the north shores of Minto Inlet that the lemming are in greater numbers now than during the earlier spring. This we noted when at the old post [Fort Collinson], Walker Bay. The same claims are made for the white fox but this might be due to natural increase from breeding.'

Other areas (*chiefly groups* 3, 9, 10 *and* 11). The evidence about the large remaining areas is less satisfactory because of the small number of observers and comparative rarity of some or all of the three species. Events in the coastal areas and interior of James Bay and southern Hudson Bay and in the huge expanse of land from the west coast of Hudson Bay to the Mackenzie Delta are not easy to describe from rough numerical data and will have to be treated in less general outline in some future paper. Particular attention will have to be paid to the effects of migration, especially in those areas outside the normal breeding range of the arctic fox. Reports for 1939–40 showed a general scarcity of all species but the following remarks are of interest:

Belcher Islands. 'Foxes and snowy owls have been exceptionally scarce this year, which is, we believe, one reason why the lemming have been able to increase.'

Coppermine. 'No lemmings were observed right at Coppermine, but it is reported that there was a great scarcity from last year up till the late winter when quite a number were observed both on the land and out on the ice, so that they had evidently migrated here. The direction of migration was not noted, but it seems evident that they came from the mainland and were going north. Wild mice were exceptionally abundant in the immediate vicinity of Coppermine during last summer, winter and this spring. No migration was noted and there are still many mice here.'

26. *Fort Reliance.* 'Have received information that a great migration of lemming was seen in the Musk-Ox Lake district during the month of April 1940, and that the migration came from the northeast.'

The lemming cycle. In every one of the years between 1935 and 1940 lemmings (including 'mice') have, in some region or other, been reported as increasing by all or nearly all observers. Where this virtual unanimity about increase was followed by a year of similar agreement about decrease it may be assumed that a peak in numbers was reached and passed. By this criterion peak years have occurred in succession as follows:

Peak year	Region	Following peak
1935–36	Southampton Island, Repulse Bay, Chesterfield Inlet	?1939–40
1936–37	Tavane, Nonala, Eskimo Point	—
1937–38	Northern Quebec, Baffin Island, Fort Ross, King William Island, Cambridge Bay	—
1938–39	Northern Labrador, West Coast Victoria Island	—

Since, in the first region, lemming increase was reported in the three years after 1936–37 it is possible that a drop in numbers may already have occurred in 1940–41; but, in any case, the length of this cycle will have equalled or exceeded four years. The evidence about the various degrees of lemming abundance in 1939–40 suggests that the next peaks may occur in about the same order.

The cycle in arctic fox and snowy owl. There has been a general correlation between the changes in foxes and snowy owls and those in lemmings, but more precise information is needed before the many exceptions to a simple predator-prey relationship can be understood. It is unfortunate that snowy owls are in places so scarce at all times that reports about them are not always reliable.

Although fluctuation in the Eastern Arctic catch of white fox is generally termed the four year cycle, intervals as small as two and as great as six years may occur between peaks. On historical evidence the peak in fox catch may sometimes be expected in the same year as the peak in lemming numbers; sometimes one year later (Elton, in press), when starving foxes can be attracted to the baits in large numbers. Quite possibly there may be a critical time during the winter before which failure of the lemmings spells quick disaster for the foxes, while survival of the lemmings until late in the spring may support them until enough other food becomes available to carry them through to the next season. Soper (1928, p. 35) states: 'Towards spring, the foxes frequent the tide-formed ice crack along the coasts, possibly for the purpose of eating the seaweed which here and there has been brought to the surface. During March and April, the foxes capture very many of the helpless young of the ringed seal in their snow dens on the ice.'

These alternative food supplies, together with patchiness in lemming abundance and migration of the foxes, complicate a relationship which it may well be beyond the scope of present methods to establish. However, it is probable that even a slight increase in the accuracy of the reports about lemming abundance would prove exceedingly profitable, and this is borne out by our lack of knowledge about the exact time when the lemmings died off on Baffin Island during 1937–38.

For this year *as a whole* all observers but one reported lemmings as increasing or still abundant. At Lake Harbour both observers stated that lemmings decreased in the latter half of this period, and at Pond Inlet one man stated 'No change, very abundant; decrease in spring', while the other, evidently impressed more by events in the spring than in the previous months,

simply stated 'Decrease'. The reports for the same year about snowy owls showed that a definite decrease had begun, and it is probable that this was caused by a greater shortage of lemmings than some observers suspected. Part of the reason for the failure of the 1938–39 trapping season may therefore have been that lemmings became scarce too early in the previous winter.

Sledge dogs. The last two reports described a serious epidemic of 'distemper' which occurred in the Mackenzie River valley early in 1938 and swept across the Arctic from the Delta in June 1938 to Pond Inlet and Repulse Bay in May 1939. Early in the period covered by the present report this epidemic fortunately died out without greatly extending its limits. In the course of its journey of over 1500 miles the disease caused immense loss and hardship, for it is no easy matter to find replacements when all neighbouring teams are similarly depleted. So serious was the situation at Fort Ross that it was necessary to transport dogs in the *Nascopie* from as far away as the south of Baffin Island.

Dog teams at Clyde River, the next post east of Pond Inlet, did not become infected. This, the post manager stated, was because communication between the two posts stopped after disease arrived at Pond Inlet. The constable at Pond Inlet added the following information.

'This epidemic started on King William Island and was brought as far as Pond Inlet by travellers with infected dogs. No natives were allowed to travel from Pond Inlet to the east coast and any native who arrived from the east coast was made to remain here until the disease had been checked. Thus the native dogs on the east coast were not infected. All the natives east had plenty of dogs, whereas the natives west and south of Pond Inlet (Tay Sound, Eclipse Sound, Milne Inlet, Admiralty Inlet) were handicapped by a scarcity. One camp in the vicinity of Pond Inlet had only five dogs to make up a team and these were used by the community in hunting seals and foxes.'

Apart from this action the reports do not mention what steps were taken to prevent contact between infected and healthy teams, though pending the outcome of research into prophylaxis this seems to be the only way in which future disasters can be avoided.

This outbreak occurred in some areas in the same year as the decrease in white fox, but it is unlikely that this was more than a coincidence. 'Crazy disease', probably a form of encephalitis also occurring among foxes (at the time of their disappearance), has different symptoms from 'distemper' (Elton, 1931) and seems largely to have been absent from dog teams during 1935–40.

Outside the Arctic there have been three main centres of somewhat similar epidemics of 'distemper', several adjacent posts all being affected. Losses seem to have been heaviest on the north shore of the Gulf of St Lawrence, but in the Lac du Brochet and Great Slave Lake districts there were also many deaths.

Royal Canadian Air Force Photograph. Reproduced by permission.

Phot. 1. View from the air, of part of Richmond Gulf, N.W. Quebec Peninsula, with the mouth of the Clearwater River, and hills inland. This is typical barren ground country, with woods concentrated in the valleys, transitional zone between the northern conifer forest belt and pure Arctic tundra. The chief fur-bearing animals are the arctic fox and the coloured fox.

Face page 192

3. METHODS

The collection of information from the Arctic is complicated by the difficulties of travel and communication, although a network of radio stations now enables the Hudson's Bay Company to obtain up-to-date reports even from the remotest posts (Horner, 1938, 1939).

Fur returns give useful information when they become available several years later but they still have to be studied in conjunction with factors like the food of the fox, for which there are no such returns. *Scientific work* at permanent Arctic field stations is obviously a desirable goal; and the release of marked foxes as done, on a small scale, in Russia (Krasovskii, 1935) is the only way in which knowledge about migration can readily be advanced. Periodic scientific expeditions, valuable as they are, cannot take the place of long-term research. As a start much could be learned from objective data (comparable to meteorological readings) collected by some of the residents; but research would be required to develop the appropriate census methods. *Opinions* of men stationed in the Arctic, though naturally a less reliable alternative, have proved to be extremely valuable and are at present the only means of conducting a study which covers thousands of square miles and deals in units of at least three or four years.

Apart from errors inherent in subjective data there are several factors which increase the difficulty of the observers in making out their returns. (1) *Length of the period.* The forms ask for a comparison of one year with another; yet within the 12 months great changes may occur. This, as already noted, happened in 1937–38 among lemmings at Pond Inlet, and as a result two observers gave estimates which appear in the summaries of opinions as conflicting evidence. It is thus a weakness of the present way of collecting and adding up the information that too long a period is covered, and it may prove necessary to ask for two replies each year. (2) *Fur returns.* With the fox there is the difficulty that comparison may be based either on fur returns or on other evidence. Reports have already been quoted which show the difficulty of trapping fox when plenty of natural food is available, and as a result the population may wrongly be reported more abundant in some following year when better catches result, not from an increase in foxes but from a decrease in lemmings. A report from Lake Harbour shows how the 1939–40 estimate of comparative abundance (*decrease*) was based on the fur return rather than on other criteria which seemed to indicate *no change.*

Lake Harbour. 'White fox returns are just under two-thirds of Outfit 269 [1938–39] but native reports lead us to believe that foxes were as plentiful as in that outfit. However, trapping conditions were such that it was impossible for the natives to attend their traps with any degree of regularity.'

(3) *Defects of the comparative method.* At all settlements there is a gradual replacement of personnel as post-managers, police and others go out on leave;

so that some of the reports are not based on personal knowledge of the preceding year. Although there is seldom any difficulty in finding out from the natives what *changes* have occurred among the animals it is likely that the reports on *density* ('scarce', 'abundant', 'neither') must be considerably influenced by the observer's experience at other posts. It has, in fact, often been found that one year's report such as 'Increase, abundant' was followed by one of 'Increase, neither' and that estimates of density are less consistent than those of change. Thus, even with entirely accurate reports about changes it is not easy to distinguish the large from the small, still less to give them statistical expression. (4) *Size of the area.* Compared with the enormous area and with the importance of the problem there are far too few observers. Repulse Bay, for example, is 250 miles from Chesterfield Inlet, and Southampton Island has an area of 17,000 square miles; yet the full extent of our data is that provided by three observers.

These objections have been stated to show the limits of our claims to accuracy and to suggest possible ways of improving the methods of collecting and analysing the data; for it is certain that the results obtained on the present system are promising enough to warrant a considerable expansion of effort. This standard way of collecting the data is itself a vast improvement on the time when such information as was written down at all had to be extracted from a mass of other records.

4. Acknowledgements

We wish to thank the staff of the Northwest Territories Administration, Ottawa, for their great co-operation during the five years, and in particular the Commissioner of the Northwest Territories, Dr Charles Camsell, and the Deputy Commissioner, Mr R.A. Gibson. One of us (D.C.) was also privileged to accompany the 1939 Eastern Arctic Expedition in the R.M.S. *Nascopie* and so to meet a number of people whose help and information it is also wished to acknowledge. To the Governor and Committee of the Hudson's Bay Company this Bureau owes a debt of long standing for the continued supply of information and generous permission to publish it; also to Mr R.H.G. Bonnycastle and others at Hudson's Bay House, Winnipeg, who have taken a great deal of trouble in collecting the reports.

We are also very grateful to the observers themselves, on whom the accuracy of our conclusions ultimately depends, and especially to those who supply the more detailed information so useful in reconstructing the story of events at this great distance. Finally, we acknowledge the financial support of the Hudson's Bay Company and of the Carnegie Corporation of New York (through the Carnegie Institution of Washington), without whose grants the work at Oxford would probably have been discontinued.

5. SUMMARY

1. Eighty-five replies to questionnaires about changes in numbers of lemmings, arctic fox and snowy owls have been mapped and analysed for the year 1939–40. Generally speaking there was a comparative scarcity after recent decreases in numbers.

2. A review of the evidence for 1935–40 shows some striking regional differences in the years in which lemmings and 'mice' reached a peak: for this seems to have occurred somewhere in each of the five years. According to reports about the Eastern Arctic, the first peak occurred in the north part of Hudson's Bay and was followed by one on the west coast. In 1937–38 there was a peak on Baffin Island and in Northern Quebec, then a year later in Northern Labrador. It may be that in the first of these regions another peak occurred in 1939–40 after a four-year interval.

3. Arctic fox and snowy owl populations have in many areas shown a rise and fall correlated with the lemming cycle, but the data are not sufficiently precise to establish the interrelations in detail.

4. It is suggested that information about the exact time of year when decrease occurs in the lemmings may partly explain differences in the subsequent length of survival of the fox populations.

5. The severe 1938–39 pandemic of dog disease was apparently checked by quarantine measures at Pond Inlet during 1939 and did not spread much beyond its previous limits here and at Repulse Bay.

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7. Appendices

Table 1. *Summary of original data on arctic fox, lemmings, 'mice', snowy owl and sledge dog (part) for* 1939–40

The following abbreviations are used: I. = increase, D. = decrease, N. = no change, s. = scarce, a. = abundant, × = neither.

Sledge dogs: 0 = disease reported absent. 0* = slight disease or starvation reported, + = more serious disease; details in Table 3.

Square brackets indicate observations that have been partly or entirely omitted from maps or Table 2: (1) Parts or all of some areas are not mapped if they are certainly outside the animal's range; (2) In groups 2 and 3 reports from inland posts are not mapped fully or included in Table 2; (3) Reports on 'mice' and events at special time of the year are not included in the maps or in Table 2.

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company.

	Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
Group 1. Northern Labrador coast					
Frenchman's Island, outside islands and 20 to 30 miles inland	D. s.	[D. s.]	D. s.	D. s.	0
Cartwright, halfway both to Frenchman's Island and Rigolet and 80 miles inland. (W.J.C.)	none	—	D. ×	none	0
Rigolet, south 50, north 75, west 35 miles. (G.B.)	D. s.	none	D. s.	D. ×	0
Northwest River [and inland 500 miles]. (J.E.K.)	D. ×	—	D. ×	—	0
Makkovik, 50 miles north and south [and inland, north and north-west, 100 miles from post.] (H.L.) ...	D. s.	D. s.	D. s.	N. s.	0
Hopedale and 30 miles radius. (C.W.C.)	D. s.	—	D. s.	N. s.	—
Davis Inlet and 30 miles radius. (W.R.B.)	D. s.	D. ×	D. ×	D. ×	0
Nain, north 35, south 30 miles; north and north-west 75 miles; coastal islands	D. s.	D. ×	D. ×	D. ×	0
Nutak and 25–35 miles radius ...	—	D. s.	N. a.	D. s.	0
Also 100 miles west	D. s.	—	—	—	—
Hebron Bay; Saglek Bay and north-west 40 miles; Napartok Bay and south-west 90 miles. (S.E.D.) ...	D. s.	D. s.	D. s.	D. s.	—
Group 2. Coast of Northern Quebec, south to Richmond Gulf [and inland]					
Georges River and 50 [to 150] miles radius; also north to Port Burwell ...	D. s.	D. ×	I. ×	D. s.	0
Fort Chimo to Georges River, to mouth of Koksoak River and north-west 30 miles; inland 80 miles. (D.A.W.) ...	D. s.	I. a.	I. ×	D. s.	0
[Fort Mackenzie and 120 miles radius]	[D. s.]	[N. s.]	N. s.	—	—
Leaf River, Leaf Bay and coastal area 40 miles east	D. ×	I. a.	I. ×	I. ×	0
Payne Bay and 300 sq. miles. (W.E.S.)	I. ×	I. a.	I. a.	I. a.	0*
Diana Bay: from Payne Bay and River north to Cape Hopes Advance and Burgoyne Bay. (L.W.)	I. ×	I. a.	N. ×	I. a.	—
Stupart Bay to King George Sound and Burgoyne Bay [inland 150 miles]. (M.L.M.)	D. s.	I. ×	—	I. ×	0
Sugluk West and 50 miles radius. (R.C.)	D. s.	I. ×	I. a.	D. s.	0
Wolstenholme; east to within 20 miles of Sugluk, south 72 miles to Kovik River. (J.C.T.)	D. s.	D. s.	D. s.	N. ×	0

Table 1 (*continued*)

		Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
	Cape Smith, inland 50, south 20 and north 70 miles. (G.W.)	D. s.	I. ×	I. ×	I. ×	—
	Povungnetuk to Cape Anderson and Mistake Bay [inland to Long. 75°]. (J.G.C.)	D. s.	D. ×	—	D. ×	0
	End of May	[I.]	[I. a.]	—	—	—
	Port Harrison, north to Koklak River, south to Nastapoka River [and inland to watershed]. (A.B.F.)	D. s.	I. ×	I. ×	I. ×	0
	Group 3. South parts of Hudson Bay, James Bay [and inland]					
	Belcher Islands. (E.H.R.)	N. s.	I. ×	none	D. s.	0
	Great Whale River north to Little Whale Point south to Cape Jones [inland to height of land]. (T.C.C.) ...	D. s.	[D. ×]	D. ×	D. s.	—
	Fort George and 50 miles radius. (J.W.B.)	D. s.	[N. ×]	N. ×	none	0
	[Kanaapuscow, north 100, south 50, east 175, west 150 miles]. (K.M.R.)	none	—	I. s.	none	—
	Mid-December, one week	a.	—	—	—	—
	[Nitchequon...and west 100 miles]. (J.S.)	[D. s.]	—	—	—	0
	Eastmain, north 50, south 20 [inland 200 miles]. (D.G.B.)	D. s.	[N. ×]	N. ×	—	0
3.	Moose Factory and 50 miles radius. (A.D.K.)	D. a.	none	—	none	0
	Albany; north to Kapisko, south 50 and inland 50 miles. (R.G.)	—	—	I. a.	—	—
	Attawapiskat, south to the Lawashi River, [150] miles inland, north to the Ekwan River. Also Agamiski Island. (A.W.M.)	D. s.	—	D. ×	D. s.	0
	Weenusk, along the coast north 80, south 60 and inland 100 miles. (T.K.G.)	I. s.	—	I. a.	D. s.	0*
	Severn, north-east to Foot River, south-east to Shakummee River and inland [half-way to Trout Lake]. (J.E.J.W.)	D. ×	—	I. ×	I. ×	0*
	York Factory and 90 miles radius ...	s.	none	I. ×	N. ×	—
	Group 4. West coast of Hudson Bay, north from Nelson River and inland					
	Churchill to Cape Churchill and north to Long Point. (A.B.V.)	D.	N.	D.	none	0
	Nueltin Lake and radius 200 miles north-east [and south] and 15 miles west. (J.A.T.)	D. s.	—	D. ×	N. ×	+
	Eskimo Point, north 30, south 80, west 50 miles. (W.C.B.)	D. s.	I. a.	I. a.	D. s.	0*
	Early fall, locally	a.	—	—	—	—
28.	Eskimo Point vicinity. (H.O.H.) ...	D. s.	N.	—	N.	0
	Padley and 8 miles radius. (D.D.) ...	D. s.	D. s.	D. s.	D. s.	0
	Tavane, from Maguse River and Lake north to Rankin Inlet and 70 miles north to Yathkyed Lake on the Kazan River. (G.W.A.)	D. s.	I. a.	—	—	0
29.	Tavane to Chesterfield Inlet. (L.W.)	D. ×	N. ×	—	N. ×	0
	Chesterfield Inlet to Daly Bay; south to Marble Island and 60 miles inland. (J.L.F.)	D. s.	I. a.	—	N. ×	0
	Baker Lake and 50 miles radius. (P.D.)	D. ×	D. ×	D. ×	D. ×	0
	April, May	—	—	I.	—	—
32.	Baker Lake to Beverley Lake and Lat. 64°–65°. (H.A.McB.)...	D. s.	D. s.	—	D. s.	0

Table 1 (*continued*)

		Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
	Group 5. Southampton Island, Repulse Bay and Melville Peninsula					
	Repulse Bay and 20 miles radius. (T.C.)	I. ×	I. a.	I. a.	I. ×	+
	Southampton Island, except coastline from Duke of York Bay to East Bay. (E.B.M.)	I. ×	I. a.	I. ×	I. a.	0
	Group 6. Southern Baffin Island					
	Lake Harbour, east to Gabriel Strait, west to Markham Bay. (J.B.) ...	D. s.	I. ×	—	I. ×	0
31.	Lake Harbour and south coast from Foxe Channel to Cape Haven. (D.P.McL.)	D. ×	I. ×	—	I. ×	0
	Fall and winter	—	s.	—	—	—
	Cape Dorset and Foxe Peninsula south and west of Koukdjuak River, Nettilling Lake, Amadjuak River and Lake. (C.R.)	D. ×	I. ×	—	D. s.	0
	Frobisher Bay (post) and from Robinson Sound round the bay to Newell Sound (P.H.C.N.)	D. s.	I. ×	—	I. s.	0
	September and November.	a.	—	—	—	—
	Pangnirtung and Cumberland Sound...	D. s.	I. a.	—	I. a.	0
	April 15–30. (S.J.S.)	a.	—	—	—	—
36.	Pangnirtung Fiord and Cumberland Sound. (J.H.D.)	D. s.	I.	—	N.	0
	Group 7. Northern Baffin Island and north. Also, Igloolik					
	Clyde River to Coutts Inlet and Home Bay	I. ×	I. ×	—	N. ×	0
	Pond Inlet, Eclipse Sound and Navy Board Inlet. (A.S.)	D. ×	I. a.	—	I. ×	+
	Summer and autumn 1939	—	s.	—	—	—
	Piling Fiord and 20 miles radius. (A.S.)	D. s.	D. s.	—	N. ×	+
35.	Pond Inlet, Bylot Island, Eclipse Sound and vicinity south to Home Bay ...	—	I. a.	—	I. a.	+
	Also Navy Board Inlet, Admiralty Inlet and south to Murray Maxwell Bay and Piling Fiord. (J.W.D.)	D. ×	—	—	—	—
	Igloolik and land enclosing north-east Foxe Basin. (J.M.S.)	I. ×	I. ×	—	D. ×	+
	Arctic Bay, all of Admiralty Inlet and Bernier and Agu Bays. (A.R.S.) ...	D. ×	I. ×	—	D. s.	+
33.	Craig Harbour, Ellesmere Island. (R.W.H.)	D. s.	N. ×	—	I. s.	0
	Group 8. Boothia Peninsula and islands west and north					
	Fort Ross, north to Port Leopold, south to Lord Mayor Bay and west to Prince of Wales Island. (L.A.L.) ...	D. s.	D. ×	—	—	0
	Until January 1940	a.	—	—	—	—
	Read Island to Lady Franklin Point and to north shore of Prince Albert Sound. (H.W.C.)	D. s.	D. s.	—	D. s.	0
	Holman Island; around Prince Albert Sound and north along coast to Berkley Point	D. s.	D. s.	—	D. ×	—
	Group 9. Pelly Bay, west to east of Coppermine River and inland to Back River					
34.	Back River, west and north to Kent Peninsula and (Group 8) Byron Bay, Victoria Island to Boothia Peninsula.	D. ×	D. ×	—	N.	0
	Sherman Inlet district. (R.J.G.) ...	D. ×	I. ×	—	I.	0

Table 1 (*continued*)

		Arctic fox	Lemming	['Mice']	Snowy owl	Sledge dog
	Group 10. Dubawnt Lake, west to Fort Rae and Fort Resolution					
	Fond du Lac: north towards Wholdaia Lake	D. s.	—	N. ×	—	—
	Stony Rapids [west 25, south 60, east 125] and north 250 miles	D. ×	—	I. ×	N. ×	—
4.	20 miles strip from Carey Lake, Dubawnt River to Granite Falls, Thelon River. (R.M.)	I.	a.	—	—	—
6.	East of Whitefish Lake to Thelon River south of Lat. 63°. (P.D'A.)	D. s.	D. s.	—	N. a.	0
	Fort Resolution and 50 miles radius ...	D. ×	[D. ×]	N. ×	N. ×	—
27.	Taltson River and 90 miles radius. (L.B.)	D. ×	none	—	N. ×	+
	Snowdrift north to Artillery Lake [south to Fort Smith]. (I.L.W.) ...	D. s.	N. ×	N. ×	—	+
7.	East and north-east of Great Slave Lake. (J.H.R.)	D.	N.	—	N. s.	+
2.	North of west end of Aylmer Lake. (G.M.)	D. s.	N. ×	—	I. ×	0
26.	Reliance district, Lat. 62°–64°, Long. 106°–110°. (R.W.T.)	D.	N.	—	none	+
23.	Fort Rae and district	D. s.	—	—	N. s.	+
	Lake Providence. (W.S.C.)	—	N. ×	—	—	—
	Fort Rae, south-east 80, north and north-east 150, [north-west 150 and north-north-west 180 miles]	D. s.	I. a.	I. a.	N. s.	+
	Yellowknife; Lat. 62°–63°. Long. 112°–116°	none	D. s.	D. ×	none	—
	Spring	—	—	a.	—	—
20.	Yellowknife, immediate vicinity. (J.E.B.)	none	N. ×	—	none	+
13.	Yellowknife. (W.C.R.)	none	none	—	D. s.	+
5.	Yellowknife. (E.G.J.)	D. s.	none	—	none	+
	Group 11. Coppermine River to Alaska					
	Coppermine and 75 miles radius ...	D. s.	I. ×	I. a.	—	—
	Until late winter	—	s.	—	—	—
	Fort Dease and east and north-east shore of Great Bear Lake	D. s.	N. ×	N. ×	N. ×	—
	Maitland Point; Liverpool Bay from Cape Dalhousie to Baillie Island. (A.G.F.)	D. s.	N. ×	I. a.	D. s.	0
30.	Liverpool Bay from Cape Dalhousie to Baillie Island. (S.M.)	D. s.	N. s.	—	D. s.	0
8.	[Arctic Red River to] Aklavik and about 100 miles each side of river. (L.C.)	N. s.	D.	—	I. s.	0*
21.	Lower Mackenzie Delta. (D.C.M.) ...	I. ×	none	—	I. ×	0
	Aklavik; Mackenzie Delta	—	—	I. ×	—	—

Table 2. *State of arctic fox, lemming and snowy owl populations in* 1939-40. *Number of observers reporting relative abundance compared with* 1938–39

	Eastern Arctic									Western Arctic					
Group no. ...	1	2	3	4	5	6	7	Total	%	8	9	10	11	Total	%
Arctic fox:															
Increase	—	2	1	—	2	—	2	7	**13**	—	—	1	1	2	**9**
Decrease	9	9	6	10	—	6	4	44	**85**	3	1	12	4	20	**87**
No change	—	—	1	—	—	—	—	1	**2**	—	—	—	1	1	**4**
	9	11	8	10	2	6	6	52	**100**	3	1	13	6	23	**100**
Lemming:															
Increase	—	8	1	3	2	6	4½	24½	**61**	—	½	1	1	2½	**14**
Decrease	5	3	—	3	—	—	½	11½	**29**	3	½	2	1	6½	**36**
No change	—	—	—	3	—	—	1	4	**10**	—	—	6	3	9	**50**
	5	11	1	9	2	6	6	40	**100**	3	1	9	5	18	**100**
Snowy owl:															
Increase	—	6	1	—	2	4	2½	15½	**33**	—	½	1	2	3½	**21**
Decrease	6	4	4	4	—	1	2	21	**45**	2	—	1	2	5	**29**
No change	2	1	1	4	—	1	1½	10½	**22**	—	½	7	1	8½	**50**
	8	11	6	8	2	6	6	47	**100**	2	1	9	5	17	**100**

Table 3. *Information about sledge dogs*, 1939–40

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received from the Hudson's Bay Company. Reports of serious disease are marked + in this table and shown by a solid circle on the map. Outbreaks apparently less serious, deaths through starvation, etc. are shown by a broken circle on the map. Absence of trouble is shown by a full circle; but names of these posts, other than those given in Table 1, are not listed. Not more than one symbol is given for each report except where indicated (2 + etc.). Fuller descriptions of some of the areas are in Table 1.

Quebec and Labrador.

\+ *Romaine.* 'An epidemic of dog sickness started about March 1st and lasted until the end of April. 60 to 75 % of dogs in this district died. Symptoms: paralysis, fits, stomach trouble, headaches.'

\+ *St Augustine.* 'A form of distemper occurred last December. Seemed to appear at Harrington Harbour, 75 miles west along the coast. Most of afflicted dogs had "fits" at short intervals until they finally succumbed. Very few recovered. Some dogs suddenly dropped dead after a fairly long run without any previous symptoms of disease. Over 50 % of dogs along the coast perished.'

\+ *Blanc Sablon.* 'Epidemic of distemper broke out January 1940 starting about 160 miles west of Blanc Sablon and gradually spreading eastward. At least 60 % of the dogs died over a coastline of 225 miles.' (W.C.N.)

Payne Bay. 'During month of March a slight epidemic broke out among the sledge dogs. Symptoms were diarrhoea and loss of appetite lasting from four to seven days, and resulting in four deaths.' (W.E.S.)

George's River. 'No evidence of disease among sledge dogs this year in this vicinity. Only deaths were due to starvation.'

\+ *La Sarre.* 'A certain number of dogs died this winter—25 % mortality. Sickness commenced about end of January. Symptoms were, as last year, coughing, running pus in nose and eyes.' (H.I.P.)

\+ *Pointe Bleue.* 'Disease amongst 15 % of dogs in January 1940. 10 % mortality.' (H.K.F.)

Woswonaby. 'Some disease of the gums and mouth which killed several dogs was reported by the natives during March.' (F.McL.)

Table 3 (*continued*)

Ontario.

\+ *Fort Hope.* 'Distemper was common among dogs and many died. Also mange was evident in some.' (J.R.P.)

\+ *Deer Lake.* 'In January a disease which was definitely distemper affected the dogs in this sector and acted upon the different animals in various ways. We saw many affected dogs and they suffered from fits, blindness, ear cankers and lung congestion. The origin is believed to be Lake Winnipeg. Mortality 90 %.' (J.L.)

Manitoba.

Poplar River. 'A few deaths this year, mostly kidney worm due to summer feeding on fresh fish. Most of the deaths occurred during the winter months.' (A.J.G.)

Norway House. 'No epidemic diseases but liver fluke appears to be taking an increasing toll year by year.'

Cross Lake. 'No disease except usual tapeworm.' (A.M.C.)

Nelson House. 'Nothing evident—only that induced by starvation as a few dogs died during January.' (E.J.S.G.)

Split Lake. 'Not more than usual.' (A.M.)

\+ *Lac du Brochet.* 'Outbreak of what appeared to be distemper occurred early in February. First cases reported from Swan River (60 miles S.W.), but disease affected whole area north to N.W.T. boundary. Miriah Lake (100 miles N.E.) most seriously affected—possibly 75 % of dogs in that area died, but they were in poor condition from want of food. Epidemic lasted about 6 weeks. Symptoms were heavy discharge from nose, laboured breathing and loss of flesh, resulting in death, usually in 3 to 5 days. Mortality at [? du Brochet] 15 %.' (A.M.) (2+.)

\+ *Misty Lake Outpost, Lac du Brochet.* 'Outbreak of what was apparently distemper occurred during February. Loss of dogs was not great, being confined mainly to dogs that were in poor condition from lack of dogfeed. The dogs went off their feed and those in poor condition seemed to sink very fast. The sickness seems to have been contagious but did not affect all the dogs in a team.' (D.R.S.)

Saskatchewan.

\+ *Cumberland House.* 'Sledge dogs suffered a mild epidemic in which several died, during March and April 1940.' (T.McE.)

Montreal Lake. 'There was no disease of sledge dogs here. Information was received that sledge dogs belonging to Wardens of Prince Albert National Park suffered a slight epidemic of distemper early last fall. It was not severe and the dogs were segregated.'

\+ *Lac la Ronge.* 'Disease in sledge dogs occurred during the months of February and March. Degree of mortality about 2 in 5. Cause or origin unknown.' (E.McL.)

Stanley. 'Some distemper among dogs during March and April. Symptoms: cold in the head.' (A.G.)

Pine River. 'A mild form of distemper attacked the young dogs towards spring but did not appear to affect the older ones. Mortality even among those sick was not excessively high, which I would estimate at approximately 25 %. No evidence of cause or origin, but first noted in dogs of trappers arriving from further south.'

\+ *South Reindeer Lake.* 'A great number of sledge dogs have died during the past year due to distemper.' (J.G.)

Middle Lake Outpost of Lac du Brochet. 'No serious sickness occurred amongst dogs although several were affected from sick dog teams which passed through from the south. Only one affected dog died, the rest recovered quickly.' (W.D.)

Table 3 (*continued*)

Alberta.

Lake Claire Outpost of Fort Chipewyan. 'During May sledge dogs took a sickness which resulted in some of them losing the power of their hind legs and finally dying.' (W.F.)

\+ *North Vermilion.* 'Distemper (?) during December: nose running, swollen throat. No trace of origin. Most die, but those that live are useless as they seem to have no stamina.' (T.F.)

Yukon.

15. *Mayo.* 'There was malnutrition and distemper, especially during the summer months particularly among Indian owned dogs. Symptoms: catarrhal products, wasting, lassitude.' (J.S.)

Northwest Territories.

1. Mackenzie River Valley

8. *Arctic Red River.* 'This year there was only one case of death which occurred early in the summer (June 1939) after the first hot days. Symptoms: stiffness in the back legs (distemper), loss of appetite. They say three other old dogs died too.' (L.C.)

2. Great Slave Lake Region

9. *Fort Smith.* 'No epidemic that I know of, although some dogs have died.' (F.C.)

\+ **37.** *Fort Resolution.* 'Distemper occurred in March and a few dogs died. They had running noses and watery eyes.' (C.J.L.)

\+ **7.** *Fort Resolution.* 'There was an epidemic of disease, symptoms of which were running nose and eyes, drowsiness, loss of appetite, during February in regions around Great Slave Lake.'

\+ **27.** *Fort Resolution.* 'Epidemic of disease believed to be distemper occurred this year, and was at its height in April and May. First serious epidemic in six or seven years. Matter forms in large quantities in nose and eyes. Dog refuses to eat and weakens rapidly. Dog may be sick for 6 or 8 weeks but generally survives if not dead 10 days after first infected.'

\+ *Rocher River.* 'Distemper among sledge dogs in March, presumably brought in from South.'

\+ **10.** *Rocher River.* 'There was distemper among young dogs during January to March. Symptoms: pus from eyes and nose, and weakness. Many dying.' (D.J.B.)

\+ *Snowdrift.* 'From mid-January on, reports have been coming in about a number of young dogs sick or dying from distemper; but the outbreak, if such it may be called, has not been localized and about 23 dogs in all died. No evidence of cause or origin.' (I.L.W.)

\+ **26.** *Fort Reliance.* 'During the past few months a number of dogs have died of distemper. It was first noticed among the Native dogs and later several of the white trappers noticed it. Dogs had matter running from eyes and nose.' (R.W.T.)

\+ **13.** *Yellowknife.* 'Epidemic in October. Symptoms: running nose, weakness and thinness.' (W.C.R.)

\+ **20.** *Yellowknife.* 'There was a mild attack of distemper in February, affecting dogs of both Indians and whites—in all about 250 dogs. Dogs showed a general lack of vitality and had [? streaming] eyes and nose.' (J.E.B.)

\+ **5.** *Yellowknife.* 'Epidemic began in January and is still prevalent. Symptoms: running at the nose and sometimes dogs seem to go crazy towards last day.' (E.G.J.)

\+ *Fort Rae.* 'An epidemic appeared amongst young dogs during the month of April. There were approximately one hundred dogs lost in this area, all affected succumbing to the disease. Origin is not known. Symptoms: running sores around the eyes, loss of appetite, swollen stomach followed by partial paralysis of the hind quarters.'

\+ **23.** *Fort Rae.* 'Disease commenced in Rae District after 1 January 1940 and attacked mostly young dogs. Symptoms: weakness, inability to eat, difficult breathing.' (W.S.C.)

19. *Fort Simpson.* 'One or two dogs have died as a result of some disease but there has been no epidemic.' (W.J.G.S.)

3. Melville Peninsula Vicinity

\+ *Repulse Bay.* 'Dog disease reported last year continued until beginning of August 1939. Total mortality roughly 75 %.' (T.C.)

Table 3 (*continued*)

\+ *Igloolik.* 'In the spring, 1939, an epidemic occurred among sledge dogs and a great many died. The natives report that symptoms noted were, a tendency to run around wildly, pus running from the eyes. The epidemic affected dogs from Arctic Bay in the north, to at least south of Repulse Bay.' (J.M.S.)

4. Large Islands

\+ *Arctic Bay.* 'Since the ending of the 1939 epidemic in August, no further disease has occurred.' (A.R.S.)

\+ **35**. *Pond Inlet.* 'Epidemic occurred in June and July 1939. Started on King William Island and was brought as far as Pond Inlet by travellers with infected dogs. Symptoms: diarrhoea, paralysis of limbs, vomiting and loss of appetite, difficulty in breathing, pus from eyes and nose. Eyes became glazed and took on a peculiar greenish tinge, the pupils enlarged and blindness set in.' (J.W.D.)

\+ *Pond Inlet.* 'Dog disease occurred here about end of May or 1 June 1939. Symptoms: coughing, running nose, blood coloured excrement. Death sometimes followed from suffocation or haemorrhage. Probably 60 % mortality. Disease brought by travellers from Western Arctic to Somerset Island, Arctic Bay and on to Pond Inlet.' (A.S.)

\+ *Piling Fjord sub-post of Pond Inlet.* 'Disease occurred in August 1939. Pus from nostrils, sore feet. 60 % mortality. Disease carried from Western Arctic, Fort Ross, Arctic Bay, Ponds and Igloolik.' (A.S.)

Hudson and James Bay and Inland.

Moosonee. 'One dog died in March, cause reported to be distemper. No general outbreak.' (R.T.)

Weenusk. 'One case diagnosed as distemper in young bitch. Filmy gathering in eyes, no appetite, very emaciated. Recovered in April.' (T.K.G.)

Severn. 'No evidence of disease among the local dogs. One or two have died during the season, but I believe from overwork and starvation. There are very few dogs amongst the Severn Indians and they, with a few exception, are of very poor quality.' (J.E.J.W.)

Eskimo Point. 'No disease among sledge dogs. Many died in Padley area owing to lack of food.' (W.C.B.)

\+ *Nueltin Lake.* 'Chipewyan Indians reported losing dogs in March. Post dogs developed a white eye discharge in April and lost weight, nearly 25 % in two weeks. One dog shed hair and gave off a white skin scale very like dandruff.' (J.A.T.)

THE BREEDING DISTRIBUTION, HISTORY AND POPULATION OF THE FULMAR (*FULMARUS GLACIALIS*) IN THE BRITISH ISLES[1]

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(*With Plates* 4–8 *and* 18 *Figures in the Text*)

CONTENTS

	PAGE
1. Introduction	204
2. The investigation	205
(*a*) The 1934 questionnaire	205
(*b*) Literature	206
(*c*) Distribution of observations in time	206
(*d*) Distribution of observations in space	208
(*e*) Analysis of results	209
3. The position, status and history of the fulmar stations in Britain	210
4. Conclusions about the spread	223
(*a*) The stations	223
(*b*) The population	229
(*c*) St Kilda and the spread	235
(*d*) The fulmar abroad	238
(*e*) Some mathematical considerations	240
5. Some biological attributes of the fulmar	242
(*a*) Climatic correlations of the present distribution	242
(*b*) Breeding habitat selection	244
(*c*) Colony establishment, social effect of numbers, and the breeding season	250
(*d*) Enemies of the fulmar	256
(*e*) Food relations	256
6. The future of the fulmar in Britain	258
7. Summary	259
8. Acknowledgements	261
References and list of informants	261

1. Introduction

The fulmar (*Fulmarus glacialis glacialis* (L.)), breeds nowhere farther south than in the islands of Britain. In this country it has been known to ornithologists since the earliest times, but until the later part of the nineteenth century they thought of it as an Arctic bird which had established a large outpost in the islands of St Kilda; and as a winter visitor (particularly in November) to most of our coasts. Since that time its breeding distribution

[1] Publication of the British Trust for Ornithology.

and population have undergone changes of the same order as those of the human population of Britain since the Industrial Revolution. This paper is an attempt to give a comprehensive account of these changes (up to 1939) and to examine several problems arising out of them.

Since 1878, when the first fulmar breeding colony outside St Kilda was established on Foula, in Shetland, ornithologists have kept a more or less careful watch on the establishment of new colonies in other places. In the early years, though there was certainly room for error, it can be taken that they gave a good account of the fulmars; and there is every reason to believe that the first important stocktaking of the known colonies, that of Harvie-Brown (**113**, **114**) was extremely accurate. Since then, notes on new extensions of range have appeared regularly in journals, and general statements such as those of the *Practical Handbook* (**795**) and of Gordon (**295**) have kept interest alive. The account in the new *Handbook of British Birds* (**268**, see also **267**, **269**, **270**) is based on the preliminary results of the inquiry here described.

The establishment of the British Trust for Ornithology in 1933, as an organization devoted to co-operative field-work on birds on a national basis, provided an excellent opportunity for a full inquiry into the fulmar's distribution, the results of which could usefully be combined with the considerable mass of material in the literature. The inquiry was conducted in 1934, with G. Waterston as organizer, and by the end of that year a great deal of information had been collected. However, owing to an increase in his other activities, Waterston was unable to complete the preparation of the report, and in 1938 he handed all the documents over to Fisher. Meanwhile, a large amount of further information had come in, and with the object of gathering still more, Fisher took part in a yacht journey between Orkney and St Kilda in the summer of 1939. He also continued correspondence with observers up to, and including, the 1939 breeding season, and is responsible for the final draft and arrangement of this report.

2. THE INVESTIGATION

(*a*) *The* 1934 *questionnaire*

This was circulated to members of the British Trust for Ornithology, to members of various local societies, and to many private individuals, including lighthouse keepers, coastguards and fishermen. In addition, appeals for help were published in *British Birds* and in the *Scottish Naturalist*. Observers were asked:

(1) The name and position of every station known to them.

(2) Its description, including (*a*) nature of site, (*b*) height above sea-level, (*c*) whether coastal or inland.

(3) The year in which the fulmar was first seen in the neighbourhood of the station in the breeding season.

(4) The year in which the first eggs or young were definitely seen; the number of pairs that were then present.

(5) The approximate number of pairs that bred in 1934.

(6) Details of any apparently suitable sites where fulmars did not yet nest; and notes on any stray birds seen during the breeding season.

Of those who replied to the questionnaire or to later correspondence, 172 gave useful or new information.

(*b*) *Literature*

All available books, notebooks and periodicals, including non-ornithological publications and some newspapers, were thoroughly searched for past references to the fulmar. All the literature cited in the bibliography has been seen personally by Fisher.

(*c*) *Distribution of observations in time*

It has often been suggested that any assessment of an animal's distribution must be governed partly by a factor derived from the amount of observation devoted to it, from one time to another, or from one place to another. To examine this in the case of the fulmar, an 'observation' was considered to have taken place when a station[1] was visited in any year and remarked upon, either in the literature, or in correspondence. Table 1 shows the total number of (station year) observations in each period of five years since 1875–9; the number of breeding colonies recorded in the last year of each of these five-year periods; and the 'percentage observation' for each of these periods, a figure made up by 100 o/b—where o is the mean number of observations made yearly in the five-year period $(n-4)$ to n, and b is the number of known breeding colonies in the year n. Figs. 1 and 2 are constructed from this table.

Table 1

Five-year period	No. of observations	No. of breeding colonies	% observation
1875–9	8	2	80·0
1880–4	11	2	110·0
1885–9	11	4	55·0
1890–4	12	5	48·0
1895–9	27	10	54·0
1900–4	34	20	34·0
1905–9	48	29	33·1
1910–14	90	54	33·3
1915–19	54	62	17·4
1920–4	81	80	20·3
1925–9	107	98	21·6
1930–4	271	139	39·0
1935–9	292	208	28·1

[1] A *station* should be understood as any place suitable for a fulmar to breed, which has been discussed as such, irrespective of whether the bird has bred. A *colony* is a station where the birds are present and obviously 'interested' in the breeding season, though not necessarily proved to have bred. A *breeding colony* is a colony where the birds have been actually proved to breed, or where they can be inferred to have bred without any reasonable doubt.

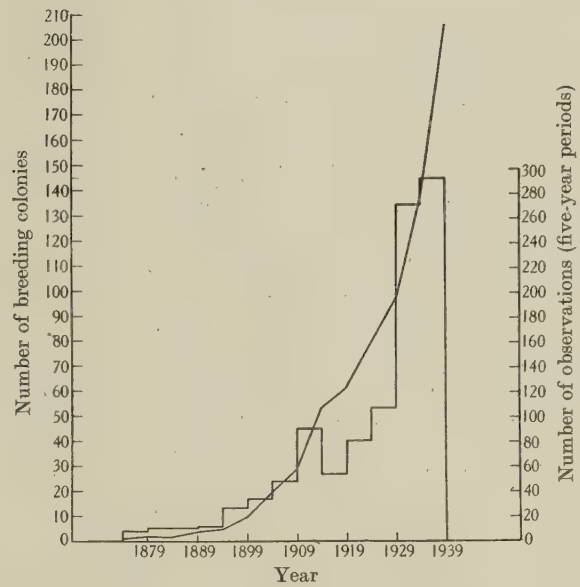


Fig. 1. Number of observations compared with number of known breeding colonies.

Fig. 2. 'Percentage of observation' against time.

From an examination of Fig. 1 we can conclude:

(1) That the gross number of observations has risen year by year since the late seventies, but not regularly. Abnormally large numbers of observations took place in 1880–9, 1910–14 and 1930–9. The first of these periods corresponds to a burst of ornithological tours in the north of Scotland, resulting in a good deal of negative evidence. The second corresponds to a period of observations which led to, or were stimulated by, Harvie-Brown's (**113**) summary, and the third corresponds to the British Trust inquiry.

(2) That the apparent drop in the increase in the number of known breeding colonies between 1915 and 1919 accompanies, and may be partly a result of, a large drop in observation during the period of the last European War.

From Fig. 2, however, we can conclude:

(3) That in relation to the number of breeding colonies that existed, the period 1880–4 was productive of the most intensive observation of all time. This serves, of course, to accentuate the value of the important negative evidence gathered at this time, mainly at stations where colonies were established some twenty or more years later. The second peak, round 1899, corresponds to a period when lighthouse-keepers and others, mainly in Shetland, were encouraged to send in annual reports for the 'Reports on Scottish Ornithology' which had begun to appear in the *Annals of Scottish Natural History* (now *Scottish Naturalist*); naturally the fulmar, new to them as a breeding bird, attracted their regular attention.

After this there was a steady drop in the relative amount of observation; by 1925 it can be imagined that in many of the fulmar's (by then numerous) breeding zones familiarity had bred contempt for the recorded note; the Trust inquiry brought the 'percentage of observation' back to nearly 40 for 1930–4. Nevertheless, this decrease in observation previous to the inquiry has left gaps in our knowledge of many fulmar colonies which the inquiry itself has been quite unable to fill.

(*d*) *Distribution of observations in space*

The areas in which fulmar colonies are now found have been divided into those in which, on an average, each colony has been visited at least once in 2 years, 4 years, 6 years or 8 years since it was first discovered. From Fig. 3, a map on which these areas of coastline are indicated, it can be seen that the most intensive observation has taken place in England, Wales, the west Lowlands and the east of Ireland. The east of Scotland up to the Moray area has been well covered, as have the west Highlands and (somewhat to our surprise) the Outer Hebrides. The north-west coast of Ireland has been visited less frequently, and observations are fewest (per colony, it must be remembered) in the north Highlands, Orkney and Shetland (where, lately, ornithologists have been, quite wrongly, inclined to state that 'it breeds everywhere'); and—here clearly through inaccessibility—in the south-west of Ireland.

(e) Analysis of results

It was intended to make the inquiry as comprehensive as possible, not only as regards plain geographical distribution, but also as regards population. When the results came in, and when the literature was consulted, it became at once clear that population details were in many cases obscure, and in a few actually conflicting. As a result, statements of population were interpreted, not in absolute numbers, but in categories corresponding (in the cases

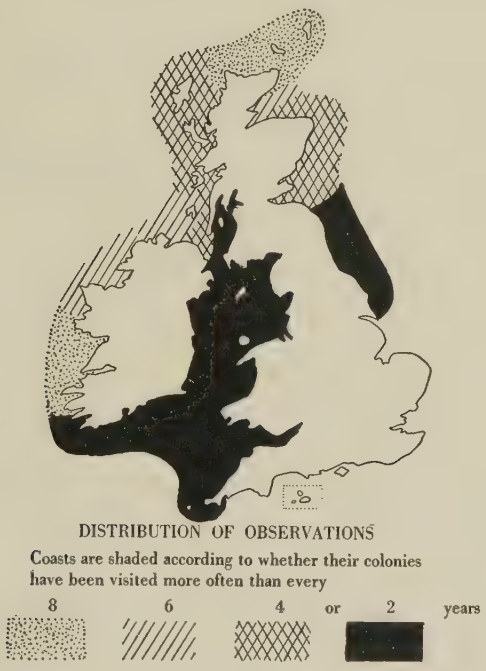


Fig. 3.

of breeding colonies) to logarithmic order. The categories finally decided upon were as follows:

–: station visited in breeding season, but no birds seen in the neighbourhood (examples in 1939: Achill Head, Stags of Broadhaven).

X: station visited in breeding season; birds seen in neighbourhood, but no evidence that they were 'interested' in or prospecting nest sites on the cliff (examples in 1939: Bills Rocks, Pig Island).

0: station visited in breeding season, and found to be a non-breeding colony (see footnote, p. 206); i.e. a station where birds were present, 'interested' in nest sites, often landing and courting, but where they could not be proved to breed, or where it could not be inferred without reasonable doubt that they were breeding. As will be discussed later, fulmars may be present at a station during the breeding season, and may alight on ledges and take up territories, for many years in succession before an egg is laid (examples in 1939: Scillies, Stack Rocks).

1: (Order 1) breeding colonies in which the birds produce under 10 eggs or chicks per year, or may be inferred without reasonable doubt to do so (examples in 1939: Farne Islands, Ailsa Craig).
2: (Order 2) as Order 1, but under 100 eggs or chicks (examples in 1939: Mull of Galloway, Tantallon Castle).
3: (Order 3) under 1000 eggs or chicks (examples in 1939: North Rona, Noss).
4: (Order 4) under 10,000 eggs or chicks (examples in 1939: Shiants, Fair Isle).
5: (Order 5) under 100,000 eggs or chicks (sole examples in 1939: St Kilda, Foula).

The present status and the history of each individual colony was examined in terms of these orders: in addition, all other information, e.g. about habitat selection, height of cliff, distance from sea, etc., and ecological relationships was analysed—largely with the use of a Paramount punch-card sorting system.

3. The position, status and history of the fulmar stations in Britain

Rules followed as much as possible in setting out the appended list of stations are:

(*a*) To use the vice-county system: the vice-counties are set out in the order of their Watsonian numbers.

(*b*) Within one vice-county, to set out the stations in order along the coast—when in doubt, clockwise—and to number them accordingly.

(*c*) To give only the bare details of each station: one copy of the complete notes, correct to 28 February 1941, is deposited at the Edward Grey Institute of Field Ornithology at Oxford, and another with the Bureau of Animal Population, also at Oxford. Fisher has kept the full index on Paramount cards himself.

(*d*) To use the place-names as given, in Great Britain, on the Bartholomew ½ in. maps. In one or two cases the spelling of these names has been altered, and in one or two others Admiralty Chart names have been used, in the absence of a Bartholomew reference.

(*e*) To use the symbols for population set out under § 2 (*e*) above.

(*f*) To use the following symbols to denote the heights and nature of the stations: u. = under, c. = coastal, b. = coastal, but a substantial beach between station and sea, i. = inland, i.e. a substantial terrain between station and sea: thus u. 200 ft. c. means under 200 ft. coastal.

(*g*) References to literature and informants are given as numbers in heavy type, referring to § 9.

Province *PENINSULA*

Vice-county 1. West Cornwall (7 stations).

1. *Scillies* (*Menavaur and Hanjague*, u. 100 ft., c.). 0:1938–9.
2. *Land's End* (u. 100 ft. c.). X:1931, 0:1936–8.
3. *Rosemergy* (u. 400 ft. c.). X:1938.
4. *Half-way between Godrevy Point and Navax Point* (u. 200 ft. c.). 0:1939.
5. *Bedruthan* (u. 400 ft. c.). 0:1939.
6. *Trevose Head* (u. 400 ft. c.). 0:1937.
7. *Stepper Point* (u. 200 ft. c.). 0:1939.

(2, 653, 801, 813, 815, 835, 948.)

Vice-county 2. EAST CORNWALL (1 station).

1. *Pentire Point to Rumps Point* (u. 400 ft. c.). X:1936, 0:1937–9.

(653.)

Vice-county 4. NORTH DEVON (1 station).

1. *Lundy Island, North End* (u. 200 ft. c.). X:1922, 0:1935, 1939.

(207, 456, 572, 882, 918.)

Province *ANGLIA*

Vice-county 27. EAST NORFOLK (2 stations).

1. *Cromer* (u. 200 ft. b.). X:1922.
2. *Sheringham* (u. 100 ft. b.). 0:1940.

(86, 272, 315, 324, 325, 326, 328, 398, 485, 553, 708, 709, 710, 744, 848, 851.)

Province *SOUTH WALES*

Vice-county 45. PEMBROKE (4 stations).

1. *Stackpole Head* (u. 200 ft. c.). 0:1931.
2. *Stack Rocks, Flimston, and mainland opposite (Green Bridge)* (u. 200 ft. c.). 0:1931–6, 1938.
3. *Skokholm* (u. 100 ft. c.). 0:1931, 1933–4, 1936–9.
4. *Strumble Head* (u. 100 ft. c.). X:1930, –:1934.

(133, 433, 436, 437, 438, 441, 537, 852, 872, 884, 885.)

Province *NORTH WALES*

Vice-county 49. CARNARVON (1 station).

1. *Great Orme* (u. 400 ft. c.). 0:1937–9.

(392, 871.)

Vice-county 52. ANGLESEY (1 station).

1. *Holyhead, near South Stack* (u. 400 ft. c.). 0:1938–9.

(802, 938.)

Province *HUMBER*

Vice-county 61. SOUTH-EAST YORKS (3 stations).

1. *Sewerby* (u. 100 ft. c.). 0:1934–5, 1:1939.
2. *Flamborough to Speeton* (u. 400 ft. c.). 0:1918–21, 1:1922–3, 2:1925–7, 1929, 1933–5, 1938–40.
3. *Filey Brigg to North Cliff* (u. 200 ft. c.). 0:1934, 2:1939.

(87, 88, 285, 316, 318, 319, 443, 448, 488, 489, 490, 603, 681, 694, 724, 726, 763, 764, 765, 766, 767, 768, 772, 812, 886, 909, 953.)

Vice-county 62. NORTH-EAST YORKS (6 stations).

1. *Redcliffe and Gristhorpe* (u. 400 ft. c.). 0:1924–7, 1933, 1:1939.
2. *Scarborough Castle Cliff* (u. 200 ft. c.). 0:1921–2, 1927–8, 1:1929–32, 2:1933–6, 1938–9.
3. *Ravenscar* (u. 800 ft. c.). 0:1935.
4. *Ness Cliffs, Robin Hood's Bay* (u. 100 ft. c.). 0:1932–4.
5. *Whitby* (u. 200 ft. c.). 0:1922–4, 1926, 1:1927–9, 1931, 1933, 1935.
6. *Huntcliffe, near Saltburn* (u. 400 ft. c.). 0:1932, 1937, 1:1939.

(6, 165, 166, 167, 169, 170, 171, 172, 173, 174, 175, 176, 177, 179, 180, 181, 182, 183, 184, 320, 321, 322, 696, 724, 765, 766, 767, 909, 928, 935, 936, 952.)

Province *TYNE*

Vice-county 66. County Durham (1 station).

1. *Marsden Rock* (u. 100 ft. c.). 0:1926, 1:1927–9, 1933, 2:1934–5, 1937.
(**150, 279, 642, 643, 883, 959.**)

Vice-county 68. Cheviot (6 stations).

1. *Craster, Cullernose Point* (u. 100 ft. c.). 1?:1928, 0:1929–33, 1:1934–6.
2. *Dunstanburgh Castle and cliffs adjacent* (u. 25 ft. c.). 0:1926, 1:1928, 0:1930–1, 1:1933–6.
3. *Bamburgh, basalt crag ¼ mile from sea* (u. 100 ft. inland). 1?:1928, 0:1931, 1933, 1:1934–6.
4. *West Cliff of Inner Farne* (u. 25 ft. c.). 0:1919–22, 1924, 1929–30, 1934, 1:1935–9.
5. *Holy Island, The Coves* (u. 50 ft. c.). 0:1923–6, 1:1928, 1935–8, 2:1939.
6. *Holy Island, Castle Rock and Lime-Kilns* (u. 50 ft. c.). 0:1936–8, 1:1939.
(**71, 84, 85, 150, 239, 285, 288, 289, 426, 427, 428, 429, 571, 572, 802, 836, 863, 883, 896, 902, 918, 952.**)

Province *LAKES*

Vice-county 70. Cumberland (1 station).

1. *St Bee's Head* (u. 100 ft. b.). –:1934, 0:1938.
(**471, 802, 818.**)

Vice-county 71. Isle of Man (8 stations).

1. *Maughold Head* (u. 100 ft. c.). 0:1938–9.
2. *Clay Head* (u. 100 ft. c.). 0:1938.
3. *Kione ny Ghoggan, Stacka to Bay ny Breechyn* (u. 100 ft. c.). 0:1931–5, 1938–9.
4. *Calf of Man* (u. 100 ft. c.). 0:1930–5, 1:1936–9.
5. *Aldrick* (u. 100 ft. c.). 0:1933, 1938.
6. *Bradda, near Fleswick* (u. 100 ft. c.). X:1933.
7. *Stroin Vuigh* (u. 100 ft. c.). X:1933.
8. *Contrary Head to Peel Castle* (u. 100 ft. c.). X:1930, 0:1931–5, 1937.
(**208, 209, 300, 301, 477, 535, 573, 591, 593, 594, 595, 597, 598, 599, 639, 787, 825, 857, 923, 970.**)

Province *WEST LOWLANDS*

Vice-county 74. Wigtownshire (4 stations).

1. *Mull of Galloway* (u. 200 ft. c.). X:1897, 0:1928–31, 1:1932–6, 2:1939.
2. *Dunman* (u. 400 ft. c.). 0:1934, 1:1935.
3. *Port Logan to Clanyard Bay* (u. 200 ft. c.). 0:1935, 2:1939.
4. *Portpatrick* (u. 200 ft. c.). 0:1935.
(**5, 679, 845, 848, 855, 873, 878, 897, 930, 967.**)

Province *EAST LOWLANDS*

Vice-county 81. Berwickshire (5 stations).

1. *Marshall Meadows to Lamberton* (u. 200 ft. b.). 0:1935, 1:1936.
2. *Burnmouth, cliffs to N. of village* (u. 400 ft. c.). 1:1934.
3. *St Abb's Head, Nunnery and Whiteheugh* (u. 400 ft. c.). 0:1915, 1920, 1:1921, 1931, 1933, 2:1934–5.
4. *Fast Castle* (u. 400 ft. c.). 1:1921, 1931, 2:1933–5.
5. *Peasedean, Swallows Craigs to Cove* (u. 200 ft. b.). 0:1927–30, 1:1932–3.
(**53, 100, 252, 429, 590, 602, 620, 728, 729, 808, 930, 967.**)

Vice-county 82. EAST LOTHIAN (4 stations).

1. *Tantallon Castle* (u. 100 ft. b.). –:1927, 0:1929, 1:1930–3, 1935–6, 2:1938–9.
2. *Bass Rock* (u. 400 ft. c.). 0:1923, 1925, 1928–33, 1935–6, 1:1937, 1939.
3. *Craigleith* (u. 100 ft. c.). X:1926, –:1933.
4. *Fidra* (u. 50 ft. b.). –:1933, 1:1938.

(**50, 309, 478, 602, 618, 620, 632, 635, 636, 797, 805, 807, 827, 848, 902, 903, 934, 953.**)

Province *EAST HIGHLANDS*

Vice-county 85. FIFE (5 stations).

1. *Inchcolme* (u. 100 ft. c.). X:1933.
2. *Inchkeith* (u. 200 ft. c.). X:1933, –:1935.
3. *Earlsferry Cliffs, Kincraig Point* (u. 200 ft. c.). 0:1933–5.
4. *Caiplie* (u. 100 ft. b.). 0:1934.
5. *Isle of May* (u. 100 ft. c.). X:1914, 0:1921–5, 1929–30, 1:1931–4, 1936.

(**43, 47, 48, 613, 620, 697, 805, 841, 842, 843, 894, 902, 930.**)

Vice-county 90. ANGUS (2 stations).

1. *Gaylet Pot to Red Head* (u. 400 ft. c.). 0:1920, 1:1921–4.
2. *Lunan, Rickle Craig to Boddin* (u. 100 ft. c.). 0:1927, 1933–4, 1:1935.

(**48, 82, 377, 422, 618, 809, 907, 930.**)

Vice-county 91. KINCARDINESHIRE (3 stations).

1. *Kirkside Graveyard* (u. 100 ft. c.). 0:1931, X:1932, 1:1934–5.
2. *Fowlsheugh* (u. 200 ft. c.). 0:1914–15, 1:1920, 1924,1928.
3. *Cove Bay* (u. 100 ft. c.). 0:1920.

(**42, 45, 48, 53, 621, 742, 809, 902.**)

Vice-county 93. NORTH ABERDEENSHIRE (3 stations).

1. *The Skares* (u. 50 ft. c.). 1:1931.
2. *Cliffs opposite Dunbuy Rock* (u. 200 ft. c.). 0:1931.
3. *Pennan Head* (u. 400 ft. c.). 0:1913, 1:1916, 2:1920.

(**115, 742, 869.**)

Vice-county 94. BANFF (1 station).

1. *Troup Head* (u. 400 ft. c.). 0:1915–16, 1:1920–1, 2:1939.

(**298, 617, 742, 929.**)

Vice-county 95. MORAYSHIRE (2 stations).

1. *Hopeman to Covesea Rocks* (u. 200 ft. c.). 0:1919, 1921–2, 1:1923, 2:1933–6, 1939.
2. *Sandstone Ravine c.* 1 *mile from sea (locality not specified)* (u. 100 ft. i.). 1:1928.

(**47, 345, 460, 608, 617, 913, 929, 937.**)

Province *WEST HIGHLANDS*

Vice-county 97. WESTERNESS (1 station).

1. *Ardnamurchan Point* (u. 100 ft. c.). 0:1933.

(**943.**)

Vice-county 100. CLYDE ISLANDS (2 stations).

1. *Pladda* (u. 100 ft. c.). X:1931, 1933.
2. *Ailsa Craig* (u. 800 ft. c.). –:1894, X:1931, –:1932–3, 0:1936, –:1937, 0:1938, 1:1939–40.

(**459, 474, 837, 847, 848, 853, 892, 901, 953, 963, 964, 965.**)

Vice-county 101. CANTIRE (1 station).

1. *Mull of Kintyre* (u. 400 ft. c.). 0:1929, 1933.

(475, 834.)

Vice-county 102. EBUDES (Inner Hebrides) SOUTH (4 stations).

1. *South Islay, including Mull of Oa* (u. 400 ft. c.). 0:1924–5, 1:1926, 1934, 2:1936.
2. *Islay, Lossit Point* (u. 200 ft. c.). 0:1934.
3. *Islay, Sanaig Cliffs (N.W.)* (u. 200 ft. c.). 1:1924, 2:1936.
4. *Colonsay, N.W. Cliffs* (u. 400 ft. c.). 0:1924, 1927, 1929, 1:1932–3.

(619, 802, 876, 877, 895, 901, 934, 956.)

Vice-county 103. EBUDES MID (5 stations).

1. *Tiree, Kenavara Cliffs* (u. 400 ft. c.). X:1906, 0:1925–6, 1:1929, 2:1933.
2. *Dutchman's Cap, Treshnishs* (u. 100 ft. c.). X:1924, 0:1927–9, 1933.
3. *Lunga, Treshnishs, Harp Rock and East Cliffs* (u. 100 ft. c.). 0:1925–6, 1:1929–32, 2:1933, 3:1937.
4. *Mull, Treshnish Point* (u. 100 ft. c.). 0:1932–3.
5. *Mull, W. side Caillach Point* (u. 50 ft. c.). 0:1932–3.

(*Mull, locality not specified*, 0:1761.)

(51, 303, 466, 740, 817, 837, 864, 887, 889, 893, 899, 926.)

Vice-county 104. EBUDES NORTH (10 stations).

1. *Muck, Cliffs east of Camas Mor* (u. 200 ft. c.). 1:1934.
2. *Eilean an Each* (u. 200 ft. c.). 0:1930.
3. *Rum, S.W. coast* (u. 800 ft. c.). X:1933, 1:1934.
4. *Rum, Dibidil Bay* (u. 200 ft. c.). X:1933, 1:1935.
5. *Sanday, Gull Rock and Gagisgor Cliffs, near The Pinnacle* (u. 200 ft. c.). 0:1929, 1:1930, 1933, 1935–6, 2:1939.
6. *Canna, North Cliffs and Garrisdale* (u. 400 ft. c.). 0:1933, 1935, 1:1936, 2:1939.

(*Skye, Minginish, near Stac a'Mhadaidh* (u. 800 ft. c.). Breeding 1871 should be attributed to Manx Shearwater.)

7. *Skye, S. of Dunvegan Head* (u. 1600 ft. c.). 1:1936.
8. *Skye, Rudha Hunish to Floddigarry* (u. 400 ft. c.). 0:1933, 1:1934–7, 2:1938–40.
9. *Eilean Trodday* (u. 100 ft. c.). 1:1938.
10. *Fladda-chuain* (u. 50 ft. c.). 0:1933–4, 1:1938.

(140, 296, 303, 467, 820, 831, 850, 856, 900, 941, 960, 967, 968.)

Province *NORTH HIGHLANDS*

Vice-county 105. WEST ROSS (3 stations).

1. *Rudha Reidh* (u. 100 ft. c.). 0:1933.
2. *Priest Island, N. and S.W. Cliffs* (u. 100 ft. c.). Fulmar bones found in kitchen-midden 1937, –:1884, X:1931, 0:1933–4, 1936, 1:1937, 2:1938–9.
3. *Bottle Island* (u. 100 ft. c.). 0:1939.

(104, 138, 219, 221, 837, 856.)

Vice-county 106. EAST ROSS (7 stations).

1. *Rosemarkie, cliffs to E.* (u. 100 ft. b.). 0:1926, 1:1934.
2. *Rosemarkie, precipitous glen ¾ mile inland* (u. 400 ft. i.). 1:1938.
3. *South Sutor* (u. 400 ft. c.). 0:1931.
4. *North Sutor to Port an Righ* (u. 800 ft. c.). 0:1926, 1929–33, 1:1934–5.
5. *Cadboll to Geanies* (u. 400 ft. c.). 0:1922, 1927, 1933, 1:1934.
6. *Rockfield Braes* (u. 400 ft. c.). 0:1924.
7. *Tarbat Ness* (u. 50 ft. c.). 0:1919, 1:1924.

(28, 227, 531, 823, 846, 880, 908, 912, 929, 972.)

Vice-county 107. EAST SUTHERLAND (1 station).

1. *Strathsteven* (u. 100 ft. c.). 0:1936–8, 1:1939.

(829.)

Vice-county 108. WEST SUTHERLAND (16 stations).

1. *Rhu Stoer* (u. 400 ft. c.). 0:1937, 3:1939.
2. *Old Man of Stoer* (u. 200 ft. c.). 2:1939.
3. *Handa* (u. 400 ft. c.). X (prob. error):1865, –:1882, 1890, 0:1898, 1900, 1902, 1:1903–4, 1906–7, 2:1912, 1925–6, 3:1927, 1939.
4. *Cow Point, Cnoc Poll a Mhurain to Rudh'an Fhir Leithe* (u. 400 ft. c.). 1:1934, 2:1939.
5. *Am Buachaille, Stack and Mainland opposite* (u. 400 ft. c.). 1:1914, 1934–5, 2:1939.
6. *Bulgach, N.W. side* (u. 100 ft. c.). –:1882, 1:1914, 1927.
7. *Cape Wrath, Clomore Cliffs* (u. 1600 ft. c.). –:1882, 0:1897, 1900, 1:1902, 1904, 2:1910, 3:1939.
8. *Garve Island* (u. 100 ft. c.). 0:1914.
9. *Fair-aird Head* (u. 400 ft. c.). –:1882, 1:1918, 2:1932, 1934–6.
10. *Whiten Head* (u. 1600 ft. c.). –:1882, 1913, 2:1935, 1939.
11. *Roan Island, W. cliff* (u. 200 ft. c.). 0:1929–31, 2:1935.
12. *Neave Island* (u. 200 ft. c.). 1:1930–1, 1935.
13. *Skerray, Ard Torrisdail* (u. 200 ft. c.). 0:1931.
14. *Strathy Point* (u. 400 ft. c.). –:1894, 1:1904, 1918, 1930, 2:1939.
15. *Strathy Cliffs, Baligill to Rudha na Cloiche* (u. 400 ft. c.). 2:1930, 1939.
16. *Cnoc Geodh Stoir* (u. 400 ft. c.). 3:1939.

(51, 61, 62, 103, 113, 118, 122, 137, 153, 198, 402, 418, 419, 495, 528, 602, 611, 663, 723, 802, 804, 806, 824, 837, 848, 849, 895, 914, 945, 953, 965, 971.)

Vice-county 109. CAITHNESS (11 stations).

1. *Red Point* (u. 200 ft. c.). 2:1939.
2. *Sandside Head* (u. 200 ft. c.). 0:1931, 1:1939.
3. *Holborn Head* (u. 200 ft. c.). 0:1905, 3:1939.
4. *Dunnet Head* (u. 400 ft. c.). 0:1900–1, 1904, 2:1905–7, 3:1931.
5. *St John's Point* (u. 100 ft. c.). 0:1923, 1:1925.
6. *Stroma* (u. 200 ft. c.). 1:1936.
7. *Duncansby Head* (u. 200 ft. c.). 0:1910, 2:1920, 1925, 3:1931, 1935.
8. *Noss Head* (u. 100 ft. c.). 0:1910–11, 1916, 1918, 1:1920, 2:1931, 1934.
9. *Gote O'Tram to Tods Gote* (u. 200 ft. c.). 2:1934.
10. *Lybster, cliffs on both sides* (u. 200 ft. c.). 1:1916–17, 2:1931.
11. *Berriedale Ness* (u. 800 ft. c.). 2:1911, 1913, 3:1931.

(29, 43, 46, 55, 112, 115, 262, 263, 282, 295, 400, 497, 546, 614, 615, 616, 807, 822, 848, 858.)

Province *NORTH-WEST ISLES*

Vice-county 110. NORTH-WEST ISLES (24 stations, including St Kilda and Rockall).

HARRIS AND LEWIS.

1. *Sula Sgeir* (u. 200 ft. c.). X (prob. error):1850, –:1883, 1:1887, 3:1932, 1939.
2. *North Rona* (u. 400 ft. c.). X (prob. error):1850, –:1883, 1885, 0:1886, 1:1887, 1894, 2:1906, 1910, 3:1914, 1931, 1933, 1936, 1938–9.
3. *Butt of Lewis* (u. 200 ft. c.). 0:1914–16, 1:1934.
4. *Rudha Geall* (u. 200 ft. c.). 0:1934.
5. *Bun Chasgro* (u. 100 ft. c.). 0:1934.

6. *Cellar Head, Doone Tower to Rudh'an-t-Seileir* (u. 200 ft. c.). 0:1911, 1:1913–15, 2:1922, 1931, 3:1934.

7. *Cellar Head to Tolsta Head, Eilean a'Bhuic to Leac Dhubh Gob Thais* (u. 200 ft. c.). 3:1939.

8. *Tiumpan Head* (u. 200 ft. c.). 0:1912, 1927, 1:1928, 1933.

9. *Rudha Ranish* (u. 200 ft. c.). 1:1939.

10. *Rudha na Creigo Moire* (u. 100 ft. c.). 1:1939.

11. *Rudha Iosal* (u. 200 ft. c.). 1:1939.

12. *Kebock Head, Creag Mhor* (u. 200 ft. c.). 2:1939.

13. *The Shiants* (u. 200 ft. c.). –:1879, 1903, 1:1910, 2:1926, 3:1934, 1936, 4:1939.

14. *Toe Head, between Toe Head and Bretasker* (u. 400 ft. c.). X:1883, 1:1934.

15. *Creag Mhor, East Loch Roag, opp. Eilean Bhinndaleim* (u. 100 ft. c.). 0:1939.

16. *Gallan Head to Budha Brataig* (u. 400 ft. c.). 2:1939.

17. *Flannan Isles* (u. 100 ft. c.). X:1881, 0:1901, 1:1902, 1904–7, 2:1913–15, 1931.

Uist and Barra.

18. *Berneray and Mingulay, including Barra Head* (u. 800 ft. c.) possibly breeding *c.* 1831. –:1844, 1865, 1868, 1870, 1894, 1898, 0:1899, 1:1902, 1906, 2:1910–11, 1918, 3:1934, 1936, 1939.

19. *Barra, Greian Head* (u. 200 ft. c.). 0:1939.

20. *Monach Islands* (u. 50 ft. c.). X:1916, –:1933.

21. *Haskeir Island* (u. 200 ft. c.). –:1881, 1:1919, 1933, 2:1939.

22. *Pabbay, Sound of Harris* (u. 400 ft. c.). 0:1929–30, 1:1932, 1935.

(For stations 1–22: **4, 24, 25, 40, 41, 42, 43, 58, 59, 61, 62, 98, 101, 102, 105, 109, 113, 119, 122, 123, 157, 161, 185, 186, 187, 188, 189, 220, 221, 245, 261, 276, 295, 303, 335, 348, 400, 418, 419, 472, 473, 509, 540, 547, 548, 611, 612, 614, 712, 713, 720, 798, 804, 831, 832, 837, 838, 848, 850, 856, 858, 866, 888, 910, 915, 916, 921, 933, 941, 953, 966.**)

23. *St Kilda* (u. 1600 ft. c.). Known to be breeding order 5:1697–1939; full discussion follows.

24. *Rockall* (u. 50 ft. c.). X (prob. error):1887, –:1896, 1921.

(**117, 286, 307.**)

ST KILDA, DETAILED HISTORY

Though St Kilda really consists of several stations which are as discrete as many of those we have been considering, it is convenient to treat it all as one. As its human history is so closely bound up with its fulmar history a review from the earliest relevant time is necessary.

About *1594* D. Monro does not mention the fulmar, but only 'wyld foullis'. About *1612* J. Moniepennie does not mention the fulmar. In *1682* G. M'Kenzie mentions wild-fowling, but not the fulmar by name. In *1697* Martin Martin found 180 inhabitants. Incidentally he provided a wonderfully accurate account of the habits of the fulmar, which he found to be present all the year round except for September and part of October. The inhabitants preferred it as an article of food to all other birds, except possibly the gannet, of which over 20,000 were said to be killed. A. Buchan, who was minister from *1705–30*, describes an increase in the human population to about 200. In *1724* (J. Sands says *1730*),

Photo C. P. Blacker, 1939

Photo 1. Conachair, St Kilda, the highest sheer cliff in Britain, 1397 ft. high; the centre of the chief British breeding-ground of the fulmar.

Photo J. Fisher, 1939

Photo 2. Conachair, the great cliff of Hirta, St Kilda, with Soay in the background and fulmars in the foreground.

Face page 216

according to K. MacAulay the islands were nearly depopulated by smallpox; only 30 survived, mainly owing to a party of 11, marooned on Stac an Armin, escaping the disease. This was not mentioned by Buchan. In *1758*, according to K. MacAulay,[1] there were 88 inhabitants and the fulmar began to replace the gannet more as the staple diet.

In *1835* the population was 3 less than it was in 1847, the year in which W. M. E. Milner paid his visit (calculated from his birth- and death-rate figures). In *1840* J. MacGillivray found whole cliff faces covered with the nests of fulmars in July, but gave no figures for either man or bird. In *1840* and *1841*, according to N. MacKenzie, about 20,000 young fulmars were hatched; 10,000 non-breeders were also present. He reckoned that 12,000 young were taken for food. In *1841*, according to J. Wilson, the human population was 105. In *1847* W. M. E. Milner estimated the human population as not over 100 and noted that it had been stationary for many years. It is not possible to calculate the number of fulmars taken from his feather statistics.

In *1851* the Government Census recorded 110 inhabitants, and J. Ritchie calculates, on the basis of 20,000 *gannets* to 180 inhabitants in 1697, that these accounted for at least 15,000 young fulmars. It should here be mentioned that the breeding population of gannets in the whole group in 1939 was about 16,900 pairs; which points to the conclusion that Martin's record of 20,000 young taken in 1697 may have been too high. About *1855*, according to J. Sands, 35 inhabitants left for Australia. In *1861*, according to G. Seton, the human population was 78. In *1864*, J. Sands records 8 persons were drowned. In *1868* H. J. Elwes recorded thousands of fulmars on Conachair, and stated that the inhabitants liked fulmars and gannets best to eat. On 22 May he took 2 fulmars' eggs on Dún. In *1871*, according to R. Gray, between 18,000 and 20,000 young were taken. This estimate is probably exaggerated. According to G. Seton, the human population in this year was 71. In *1875* J. Sands found the population to be 72, and nearly 600 gallons of fulmar oil were exported. This may represent about 9600 birds. In *1876* Sands found the human population to be 75. In *1877* J. A. Harvie-Brown recorded a great increase of fulmars, and the *Dunara Castle* started a regular service from the mainland to the islands. In *1884* C. Dixon recorded 'thousands and tens of thousands' of fulmars on Hirta. Writing in 1900, he states that 20,000 young were reputed to be taken, but it is not possible to tell whether he refers to the number taken in the year of his own visit, or whether he quoted R. Gray's highest figure for 1871—the highest previous estimate. This record, then, cannot be accepted as being of value. In *1885* (Oct.) the population was 78 (R. Connell). By *1886* R. Connell states that 'recent observations show that the fulmar is slightly decreasing in numbers on St Kilda'. The human population was 80 in June

[1] MacAulay was on St Kilda, sailing 6 June 1758 and returning July 1759. The natural history parts of his book are his own observations, and seem very accurate; the antiquarian parts, however, are by J. MacPherson, who never visited St Kilda.

and 79 at the end of the summer. In *1889*, according to D. W. Logie, the human population was about 80, and 800 young birds were taken in one day. In *1896* R. Kearton records the human population as 73, and that fowling activities went on as usual. In *1897* about 8960 fulmars were being captured every year, according to H. A. MacPherson. In *1898* N. Heathcote found the human population to be 70, and that fulmars were caught all the year round 'but not in any numbers and only in certain places'. The main breeding quarters were on Conachair. Feathers were used for stuffing mattresses.

In *1902* J. Wiglesworth found 76 human inhabitants (one was born when he was there). He said that the average number of young fulmars taken was about 7500, but that in this particularly good season the catch was about 9600. He also stated that there were more fulmars on Soay than on all the other islands of the group together. In *1903* J. A. Harvie-Brown recorded a very great increase. In *1910* W. Eagle Clarke found that about 9000 young were taken. He was a very reliable authority. In *1914* E. W. Wade found the fulmar breeding-ground 'fully occupied' and suggested that the young birds were being 'squeezed out' to Boreray and the outlying stacks, where he stated 25 % of the eggs to be addled. By this year young were only being taken on Hirta, and not on Soay, Boreray or Stac an Armin. On 23 and 26 May boatloads of fulmars were brought in, according to the Duchess of Bedford. In *1921* the human population was 80. In *1930* it was 43, and according to A. A. MacGregor, fulmars were still being killed and stored in barrels. In September St Kilda was evacuated by man. In *1931* T. H. Harrisson and D. Lack found the fulmar second only to the puffin in numbers—more crowded than on Grímsey and the Westmann Islands in Iceland, or even than on Bear Island—and, in actual population, about 25,500 breeding pairs. In *1935* the Earl of Dumfries ringed 5 adults on 'St Kilda' on 6 June, and 2 more on Dún on 12 June. In *1936* Lord Dumfries ringed one adult on Dún on 7 July.

In *1939*, from 31 May to 2 June, J. S. Huxley, E. M. Nicholson and J. Fisher found a population of about 20,780 pairs of fulmars in occupation of nest-sites, divided as follows:

	Counted direct		Estimated		
	From land	From boat	From land	From boat	Total
Hirta	5,620	—	2,500	3,650	11,770
Dún	110	—	—	1,500	1,610
Soay	—	250	—	4,250	4,500
Stac an Armin	—	400	—	—	400
Boreray	—	—	1,500	1,000	2,500
	5,730	650	4,000	10,400	20,780
	6,380 (31 %)		14,400 (69 %)		

Though the party saw no fulmars breeding on Stac Lee, it should be recorded that J. Wiglesworth, who climbed it on 10 June 1902, found 5 pairs in a wildfowler's shelter.

Photo J. Fisher, 1938

Photo 3. The Kame, Foula, Shetland. The second highest sheer cliff in Britain (1220 ft.), it lies in the centre of Britain's second fulmar colony. It is steeper than Conachair.

Face page 219

On 7 August 1939 the Earl of Dumfries ringed 4 young on Dún, and on 10 August 2 young on Hirta.

The history outlined above was used in the construction of Fig. 12 and Table 6.

(61, 109, 114, 129, 161, 199, 228, 229, 245, 303, 346, 349, 360, 379, 395, 442, 458, 461, 463, 464, 465, 467, 486, 502, 506, 507, 528, 585, 622, 660, 663, 680, 764, 785, 788, 811, 839, 848, 868, 910, 953.)

Province *NORTH ISLES*

Vice-county 111. ORKNEY (29 stations).

1. *Sule Skerry* (u. 25 ft. c.). X:1901–2, 1909, 1912, –:1914, X:1917, 0:1923–7, 1:1928, 1932–3, 1939.
2. *Sule Stack* (u. 200 ft. c.). X:1889, –:1914, 1939.
3. *Pentland Skerries* (u. 100 ft. c.). X:1912, 1914, 1928, –:1930.
4. *Swona* (u. 100 ft. c.). X:1916, 0:1925–6, –:1930.
5. *Switha* (u. 100 ft. c.). 1:1917.
6. *Hoy, S. side South Walls* (u. 200 ft. c.). 1:1917.
7. *Hoy, S. end* (u. 100 ft. c.). 0:1911.
8. *Hoy, S. and S.W. sides* (u. 800 ft. c.). 1:1917.
9. *Hoy, Old Man to Kame* (u. 1600 ft. c.). 0:1896, 1898–9, 1:1900, 2:1901–2, 1908, 3:1911, 1933, 4:1938.
10. *Mainland, Black Craig* (u. 400 ft. c.). 0:1904, 1907, –:1908, 1:1932, 1934.
11. *Mainland, Blossom Head* (u. 200 ft. c.). 1:1932.
12. *Mainland, Marwick Head* (u. 400 ft. c.). 0:1910–11, 1:1914, 2:1920, 3:1934.
13. *Mainland, Birsay to Costa Head* (u. 400 ft. c.). 0:1908, 1:1911, 2:1934.
14. *Eynhallow* (u. 100 ft. i.). X:1909, –:1922, 1:1924, 2:1932, 1934–5, 1939.
15. *Rousay* (u. 200 ft. c.). 1:1905, 2:1934.
16. *Westray, Noup Head* (u. 400 ft. c.). 1:1901, 2:1907, 1911–13, 1932.
17. *Papa Westray, Mull Head* (u. 100 ft. c.). 1:1913.
18. *Eday, Red Head* (u. 200 ft. c.). 0:1912.
19. *Calf of Eday, Grey Head* (u. 200 ft. c.). 1:1912.
20. *Sanday, Northwall, etc.* (u. 50 ft. c. and i.). 0:1918, 1:1926, 2:1933–4, 3:1935, 1938.
21. *North Ronaldshay* (u. 100 ft. i.). 1:1919, 2:1934, 3:1937.
22. *Stronsay, Burgh Head* (u. 100 ft. c.). 1:1912, 2:1927.
23. *Auskerry, East Cliffs* (u. 100 ft. c.). 1:1930–3.
24. *Shapinsay, N.E. side* (u. 100 ft. c.). 1:1939.
25. *Mainland, Deerness Cliffs* (u. 200 ft. c.). 1:1911.
26. *Copinsay* (u. 200 ft. c.). 1:1911, 2:1924–5, 3:1926–7.
27. *South Ronaldshay, Old Head to Cumla Geo* (u. 100 ft. c.). 0:1929, 1:1932–3.
28. *South Ronaldshay, The Wing to Hoston Bay* (u. 200 ft. c.). 0:1929, 1:1932–3.
29. *South Ronaldshay, the Nev to Harrabrough Head* (u. 200 ft. c.). 0:1929, 2:1932–3, 3:1939.

(38, 39, 41, 43, 53, 61, 62, 113, 131, 161, 223, 233, 235, 262, 295, 314, 403, 418, 440, 451, 452, 487, 498, 548, 561, 567, 568, 569, 612, 614, 616, 624, 626, 627, 628, 631, 654, 678, 686, 722, 738, 739, 793, 794, 822, 828, 848, 880, 881, 892, 905, 912, 930, 932, 946, 961.)

Vice-county 112. SHETLAND (68 stations).

1. *Foula* (u. 1600 ft. c.). –:1774, 0:1876–7, 1:1878, 2:1879, 1887, 1890, 3:1898, 4:1917, 1919, 5:1938–9.
2. *Fair Isle* (u. 800 ft. c.). 0:1902, 1:1903, 2:1905–7, 1909, 3:1911–15, 1923, 4:1937, 1939.

3. *Sumburgh Head* (u. 400 ft. c. and i.). 0:1905, 1:1907, 2:1918–21, 3:1937.
4. *Lady's Holm and Little Holm, Sumburgh* (u. 100 ft. c.). 1:1934.
5. *Fitful Head* (u. 1600 ft. c.). –:1891–2, 0:1900, 2:1905.
6. *Noup of Reawick, Sandsting* (u. 200 ft. c.). 1:1912.
7. *Silwick to Giltarump, Sandsting* (u. 200 ft. c.). –:1934, 2:1939.
8. *Gruting Voe, cliffs at mouth* (u. 200 ft. c.). 2:1939.
9. *Papa Stour, The Horn* (u. 200 ft. c.). 0:1890–1, 1:1892, 1895, 1898, 1939.
10. *Papa Stour, Bordie to Culla Voe* (u. 100 ft. c.). 2:1939.
11. *Papa Stour, Bragasetter to Shepherd's Taing* (u. 200 ft. c.). 2:1939.
12. *Neap of Norby, Sandness* (u. 100 ft. c.). 1:1901.
13. *Snarra Ness, Sandness* (u. 100 ft. c.). 1:1939 (2:1940).
14. *Face of Neans, Aithsting* (u. 200 ft. c.). 1:1909, 2:1925, 3:1939.
15. *Vementry, N.W. side* (u. 100 ft. c.). 1:1939.
16. *Vementry, N. side* (u. 100 ft. c.). 1:1925, 2:1939.
17. *Breiness, Muckle Roe* (u. 200 ft. c.). (1:1940.)
18. *Egilsay, Mangaster Voe* (u. 100 ft. c.). 1:1939, (2:1940).
19. *Lang Head* (u. 200 ft. c.). (1:1940.)
20. *Brae Wick* (u. 200 ft. c.). 0:1922.
21. *Eshaness Skerry* (u. 100 ft. c.). –:1934, (1:1940).
22. *Garderhouse, opposite The Bruddans to Calder's Geo, Eshaness* (u. 200 ft. c.). 0:1895, 1:1896–7, 2:1914–18, (3:1940).
23. *Moo Stack, Holes of Scraada to Blackhead of Breigeo and stack opposite Grind of the Navir, Eshaness* (u. 100 ft. c.). (2:1940.)

(*Muckle Ossa, Eshaness* (u. 100 ft. c.). –:1934.)

24. *Point of Fethaland, North Roe* (u. 100 ft. c.). 1:1905.
25. *Gruney, North Roe* (u. 100 ft. c.). 1:1905.
26. *Ramna Stacks, North Roe* (u. 100 ft. c.). 1:1897.
27. *Outsta Ness, North Yell* (u. 100 ft. c.). 0:1907, 1:1921.
28. *Blue Mull, Unst* (u. 200 ft. c.). 1:1922.
29. *Hermaness to Tonga, Unst* (u. 800 ft. c.). 0:1894–6, 2:1897–9, 1907, 1911–12, 1916–18, 3:1922, 1933, 4:1937–9.
30. *Saxavord, Unst* (u. 800 ft. c.). 1:1897–8, 3:1938.
31. *Haaf Gruney, Unst* (u. 100 ft. c.). 1:1934.
32. *Wedder Holm, Unst* (u. 50 ft. c.). 1:1934.
33. *Uyea, Unst* (u. 100 ft. c.). 0:1902, 1:1910, 1912, 2:1922, 1934.
34. *Unst, cliffs to N. of Uyeasound* (u. 100 ft. c.). 1:1912.
35. *Fetlar* (u. 400 ft. c.). 1:1902, 3:1934.
36. *Hascosay* (u. 100 ft. c.). 0:1908, 1:1937.
37. *Mid-Yell* (u. 100 ft. c.). 1:1923, 2:1939.
38. *Horse of Burravoe, South Yell* (u. 200 ft. c.). 1:1905, 2:1906.
39. *Burra Ness, South Yell* (u. 100 ft. c.). 1:1935.
40. *Ness of Cuppaster, South Yell* (u. 100 ft. c.). 2:1935.
41. *Orfasay* (u. 50 ft. c.). 1:1935.
42. *Out Skerries or Whalsay Skerries* (u. 200 ft. c.). 0:1907, 1:1911, 1914–17, 1919–20, 1923.
43. *Whalsay, islets to East* (u. 100 ft. c.). 2:1932–4.
44. *Whalsay, N. and N.E. coast* (u. 100 ft. c.). 1:1906, 1939.
45. *Whalsay, Clett Head* (u. 200 ft. c.). 0:1906, 1920, 2:1929, 3:1934.
46. *West Linga* (u. 100 ft. c.). 0:1919, 1:1920, 2:1934.
47. *Lunna Ness* (u. 100 ft. c.). 1:1939–40.
48. *Moro Ness, Lunnasting* (u. 100 ft. c.). 2:1939.
49. *Winnie Neap, Nesting* (u. 100 ft. c.). (3:1940.)
50. *Heog of Neap, Nesting* (u. 200 ft. c.). (3:1940.)

51. *Drengi Geos, Neap, Nesting* (u. 100 ft. c.). (1:1940.)
52. *Muness Neap, Nesting* (u. 100 ft. c.). (1:1940.)
53. *N. and S. Geos of Brettabister, Nesting* (u. 100 ft. c.). (1:1940.)
54. *Lingness, Nesting* (u. 200 ft. c.). 0:1913, 1:1914, 2:1934.
55. *Mull of Eswick, Nesting* (u. 200 ft. c.). 2:1939, (3:1940).
56. *Hoo Stack* (u. 200 ft. c.). X:1914, –:1934.
57. *N. and S. Isles of Gletness* (u. 100 ft. c.). (2:1940.)
58. *Bight of Vatsland, Lerwick* (u. 200 ft. c.). 0:1922.
59. *Bressay, White Hill* (u. 200 ft. c.). 1:1939.
60. *Bressay, Aithsness* (u. 200 ft. c.). 0:1908, 1:1912, 1939.
61. *Bressay, cliffs opposite Noss* (u. 100 ft. c.). 2:1939.
62. *Noss* (u. 800 ft. c.). 1:1898, 2:1908, 1922, 3:1933, 1939.
63. *Bressay, South Cliffs* (u. 800 ft. c.). 1:1912, 2:1938, 3:1939.
64. *The Knab, Lerwick* (u. 100 ft. c.). X:1902, 0:1913, 1915–17, 1919, 1:1934.
65. *Ness of Sound, Lerwick* (u. 100 ft. c.). 0:1911–12, 1:1938.
66. *Brindister, Lerwick* (u. 200 ft. c.). 0:1911–12, 1:1913, 1938.
67. *Mousa* (u. 50 ft. i.). 0:1911–12, 1:1913, 2:1934, 1938.
68. *No Ness* (u. 200 ft. c.). 2:1939.

(28, 32, 38, 39, 40, 41, 42, 43, 58, 62, 107, 113, 125, 126, 139, 158, 159, 161, 247, 262, 280, 290, 291, 302, 308, 310, 314, 359, 382, 385, 386, 387, 399, 414, 415, 416, 424, 452, 453, 499, 547, 568, 570, 588, 589, 600, 612, 614, 616, 618, 650, 661, 664, 743, 746, 777, 784, 793, 803, 819, 828, 833, 848, 854, 865, 873, 874, 879, 890, 911, 919, 926, 939, 942, 949, 953, 955, 969.)

IRELAND

Vice-county 113. KERRY (5 stations).

1. *Great Skellig* (u. 400 ft. c.). X:1889, 1906–8, –:1909, 1:1913, 2:1914–16, 3:1931.
   (*Little Skellig* (u. 400 ft. c.). –:1939.)
2. *Puffin Island* (u. 200 ft. c.). 1:1931.
3. *Inishvickillaun* (u. 400 ft. c.). 0:1937.
4. *Inish-na-bro* (u. 200 ft. c.). 2:1937–8.
5. *Tearaght Island* (u. 400 ft. c.). X:1906, 0:1917.

(33, 34, 35, 329, 440, 504, 552, 749, 750, 751, 759, 761, 801, 867, 885, 931, 965.)

Vice-county 115. CORK (4 stations).

1. *Cape Clear Island* (u. 400 ft. c.). 0:1937.
2. *Mizen Head* (u. 800 ft. c.). –:1931, 0:1935–7, 2:1938.
3. *Cow Rock* (u. 200 ft. c.). 0:1938.
4. *Dursey Island* (u. 800 ft. c.). 0:1938.

(867, 931.)

Vice-county 118. WATERFORD (1 station).

1. *Mainland* (u. 400 ft. c.). 0:1930–5.

(867.)

Vice-county 121. CLARE (1 station).

1. *Cliffs of Moher* (u. 400 ft. c.). 1:1924, 1939.

(701, 801, 940.)

Vice-county 124. WEXFORD (2 stations).

1. *Between Hook Head and Fethard* (u. 200 ft. c.). 1:1936.
2. *Great Saltee* (u. 100 ft. c.). 0:1929, 1:1930–4, 2:1939.
   (*Little Saltee* (u. 100 ft. c.). –:1934.)

(278, 376, 537, 581, 582, 583, 830, 867, 875, 884, 904, 920, 931, 947.)

Vice-county 128. Galway (3 stations).

1. *Inishmore, Aran Islands* (u. 200 ft. c.). –:1928, 0:1934–5.
2. *Skerd Rocks* (u. 200 ft. c.). X:1938.
3. *Inishshark* (u. 200 ft. c.). 2:1932.
   (*Inishbofin* (u. 400 ft. c.). –:1932.)

(651, 940.)

Vice-county 133. Dublin (2 stations).

1. *Ireland's Eye* (u. 200 ft. c.). 1:1937, 0:1938–9.
2. *Lambay Island* (u. 200 ft. c.). –:1933, 0:1935, 1:1936–8, 2:1939.

(234, 376, 885, 927, 940.)

Vice-county 139. West Mayo (12 stations).

1. *Clare Island* (u. 800 ft. c.). –:1911, 0:1935.
2. *Bills Rocks* (u. 200 ft. c.). –:1904, X:1932, 1939.
3. *Achill Head* (u. 1600 ft. c.). 0:1926–8, –:1929, 0:1930–1, –:1939.
4. *Black Rock* (u. 200 ft. c.). X:1911, 1924.
5. *Duvillaun Island* (u. 200 ft. c.). 0:1926–31.
   (*Doonamo Point* (u. 400 ft. c.). –:1939.
   Erris Head (u. 400 ft. c.). –:1939.)
6. *Stags of Broadhaven* (u. 400 ft. c.). 1:1911–13, 1928–9, 2:1930, –:1939.
7. *Portacloy, Corraduff and eastwards* (u. 800 ft. c.). 0:1907, 2:1911–12, 1939.
8. *Pig Island* (u. 200 ft. c.). X:1924, 1939.
9. *Porturlin* (u. 400 ft. c.). 0:1924, 1939.
10. *Benaderreen Cliffs* (u. 400 ft. c.). 1:1938–9.
11. *Doonbristy Pinnacle* (u. 200 ft. c.). 2:1938–9.
12. *Downpatrick Head* (u. 100 ft. c.). 1:1938, 2:1939.

(34, 273, 432, 651, 652, 737, 753, 754, 755, 756, 757, 758, 801, 816, 849, 904, 940, 954, 958.)

Vice-county 140. Sligo (1 station).

1. *Aughris Head* (u. 100 ft. c.). 2:1939.

(761, 775, 776, 777, 778, 940.)

Vice-county 146. East Donegal (2 stations).

1. *Inishtrahull* (u. 200 ft. c.). X:1911, 0:1939.
2. *Garvan Islands, Rihulla* (u. 200 ft. c.). 0:1915, 1:1925, 2:1938–9.
   (*Glengad Head* (u. 1600 ft. c.). –:1934.)

(551, 702, 718, 954, 958.)

Vice-county 147. West Donegal (7 stations).

1. *Sleive League* (u. 1600 ft. c.). –:1934, 0:1939.
2. *Tormore Point* (u. 1600 ft. c.). –:1934, 0:1937–8, 2:1939.
3. *Aranmore Island* (u. 800 ft. c.). 2:1939.
4. *Tory Island* (u. 800 ft. c.). 0:1913, 1:1924, 2:1934, 1939.
5. *Horn Head* (u. 400 ft. c.). 0:1907–8, 1910–11, 1:1912, 2:1913, 1922, 1938–9.
6. *Breachy Head, Dunfanaghy, N.W. face of 'last point'* (u. 400 ft. c.). 1:1939.
7. *Between Portsalon and Rathmullen* (u. 800 ft. c.). 1:1931.

(34, 295, 376, 432, 714, 715, 753, 755, 758, 760, 802, 906, 917, 940, 954.)

Vice-county 151. ANTRIM (7 stations).

1. *Rathlin Island, N.W. cliffs, E. and W. of W. Lighthouse* (u. 400 ft. c.). 1:1921–2, 1925–6, 2:1931, 1934–6.
2. *Fair Head* (u. 800 ft. c.). 0:1934.
3. *White Head to Ballintoy* (u. 400 ft. c.). 1:1929, 1934, 1939–40.
   (*Sheep Island* (u. 200 ft. c.). –:1934.)
4. *Whitepark Bay to Dunseverick* (u. 200 ft. c.). 1:1934, 1939–40.
5. *Port Moon* (u. 200 ft. c.). 1:1930, 2:1934, 1936.
6. *Benbane Head* (u. 200 ft. c.). 0:1934, 1:1936.
7. *Giant's Causeway* (u. 200 ft. c.). 1:1930, 2:1934–8.

(22, 66, 214, 215, 216, 225, 295, 556, 557, 703, 704, 705, 761, 861, 876, 924, 925, 950, 951.)

Vice-county 152. DERRY (1 station).

1. *Downhill Cliffs* (u. 200 ft. c.). 0:1934, 1:1939.

(136, 761, 898, 906, 951.)

4. CONCLUSIONS ABOUT THE SPREAD

(*a*) *The stations*

From the details of the history of the stations set out in the previous section we construct Table 2 (p. 224).

We may also construct, with the aid of Table 2, the following figures:

Fig. 4. Map of the British Isles showing the colonies known in 1939.

Fig. 5. } Large-scale sketch-maps of Orkney and Shetland, showing their colonies in
Fig. 6. } detail impossible in Fig. 4.

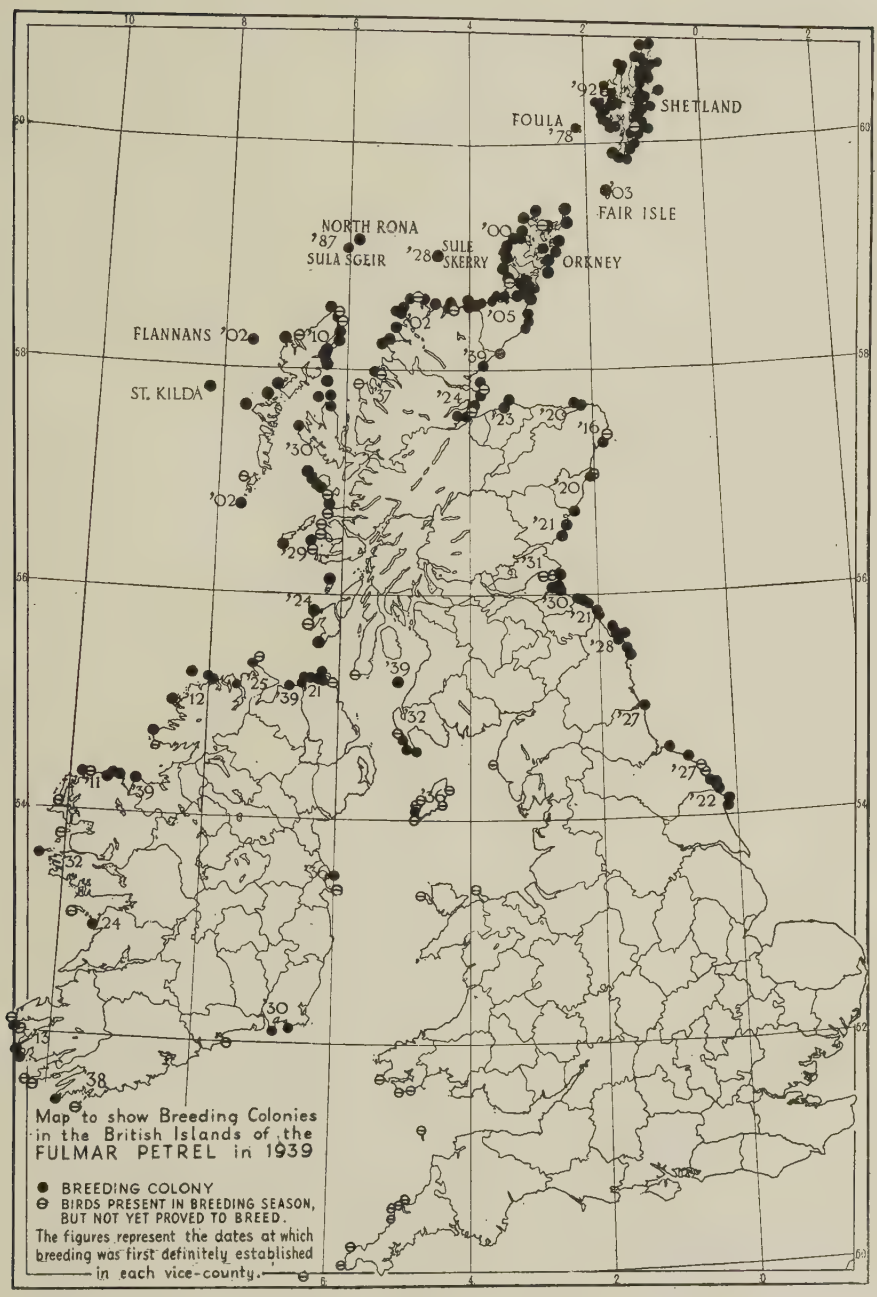
Fig. 7. Map of the British Isles showing the main directions of spread, on the hypothesis (possibly unjustified) that the spread originated from St Kilda.

We can now piece together a picture of the details and directions of the spread in space and time. If we imagine that the fulmar spread originally from St Kilda, its course can be traced in five main directions:

(1) *North-eastwards and then south* (important in relation to Norway, see p. 240). The first colony to be established outside St Kilda was Foula (Shetland) in 1878. Sula Sgeir and North Rona were colonized in 1887, and the main Shetland group in 1892, on the west, in 1897 at the north, in 1898 on the east and in 1903 on the south. Orkney was probably colonized from Shetland in 1900, and the birds' interest in the seas north of Scotland brought them to west Sutherland in 1902 (or possibly 1903). Caithness, where breeding was proved in 1905, may have been colonized from Orkney or from Sutherland. By 1916 the headland of north Aberdeenshire was reached, and the birds had 'turned the corner' of Scotland. The spread continued southwards, reaching Kincardine in 1920, Angus and Berwickshire in 1921, and by 1922 the fulmar was breeding in south-east Yorkshire (in 1940 birds first showed interest in the Norfolk coast). The increase after this has been of the nature of movement up the firths from the more oceanic headlands, ending, in the Morayshire and East Ross districts, some distance inland. In the Moray area Banff was

Table 2. *Number of breeding colonies* (*Orders* 1–5) *and non-breeding colonies* (*Order* 0) *known in each vice-county by* 1939, *and the year in which breeding was first proved in the vice-county*

			1939	
Province	Vice-county	Date of first known breeding	No. of known colonies where breeding not proved	No. of known breeding colonies
Peninsula	1 W. Cornwall	—	6	0
	2 E. Cornwall	—	1	0
	4 N. Devon	—	1	0
S. Wales	45 Pembroke	—	3	0
N. Wales	49 Carnarvon	—	1	0
	52 Anglesey	—	1	0
Humber	61 S.E. Yorks	1922	0	3
	62 N.E. Yorks	1927	2	4
Tyne	66 Durham	1927	0	1
	68 Cheviot	1928	0	6
Lakes	70 Cumberland	—	1	0
	71 Isle of Man	1936	5	1
W. Lowlands	74 Wigtownshire	1932	1	3
E. Lowlands	81 Berwickshire	1921	0	5
	82 E. Lothian	1930	0	3
E. Highlands	85 Fife	1931	2	1
	86 Angus	1921	0	2
	91 Kincardine	1920	1	2
	93 N. Aberdeen	1916	1	2
	94 Banff	1920	0	1
	95 Morayshire	1923	0	2
W. Highlands	97 Westerness	—	1	0
	100 Clyde Is.	1939	0	1
	101 Cantire	—	1	0
	102 Ebudes S.	1924	1	3
	103 Ebudes Mid	1929	3	2
	104 Ebudes N.	1930	1	9
N. Highlands	105 W. Ross	1937	2	1
	106 E. Ross	1924	2	5
	107 E. Sutherland	1939	0	1
	108 W. Sutherland	1902 (or 03)	2	14
	109 Caithness	1905	0	11
N. Isles	110 Hebrides	Immemorial	4	18
	111 Orkney	1900	2	24
	112 Shetland	1878	2	55
Ireland	113 Kerry	1913	2	3
	115 Cork	1938	3	1
	118 Waterford	—	1	0
	121 Clare	1924	0	1
	124 Wexford	1930	0	2
	128 Galway	1932	1	1
	133 Dublin	1936	1	1
	139 W. Mayo	1911	3	4
	140 Sligo	1939	0	1
	146 E. Donegal	1925	1	1
	147 W. Donegal	1912	1	6
	151 Antrim	1921	1	6
	152 Derry	1939	0	1
Total 13	48		61	208


SHETLAND
'92
FOULA
'78
'03
FAIR ISLE
NORTH RONA
'87
SULA SGEIR
'28
SULE SKERRY
'00
ORKNEY
'05
FLANNANS '02
ST. KILDA
'02
'10
'30
'24
'23
'20
'16
20
'21
'31
'30
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'28
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'32
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'27
'22
'24
'30
'38
Map to show Breeding Colonies in the British Islands of the FULMAR PETREL in 1939
BREEDING COLONY
BIRDS PRESENT IN BREEDING SEASON, BUT NOT YET PROVED TO BREED.
The figures represent the dates at which breeding was first definitely established in each vice-county.

Fig. 4.

reached in 1920, Morayshire in 1923, east Ross in 1924, east Sutherland in 1939. In the Forth area East Lothian was reached in 1930, Fife (Isle of May) in 1931. South of this the birds had spread to North Northumberland by 1928, and, possibly from south-east Yorkshire to north-east Yorkshire and Durham by 1927.

Fig. 5. Sketch-map of Orkney showing details of the known colonies in 1939, with the approximate dates of their establishment. Symbols for non-breeding and breeding colonies as in Fig. 4.

(2) *Eastwards.* Though St Kilda is nearest to the Outer Hebrides, these islands, if Sula Sgeir and North Rona be excepted, were not colonized until 1902, the same year as west Sutherland. In this year birds were found breeding on the Flannans and on Barra Head. The Shiants, on the east side, were reached probably in 1910, and Lewis in 1913. West Ross, across the Minch, was not colonized until 1937.

Fig. 6. Sketch-map of Shetland showing details of the known colonies in 1939, with the approximate dates of their establishment. Symbols for non-breeding and breeding colonies as in Fig. 4.

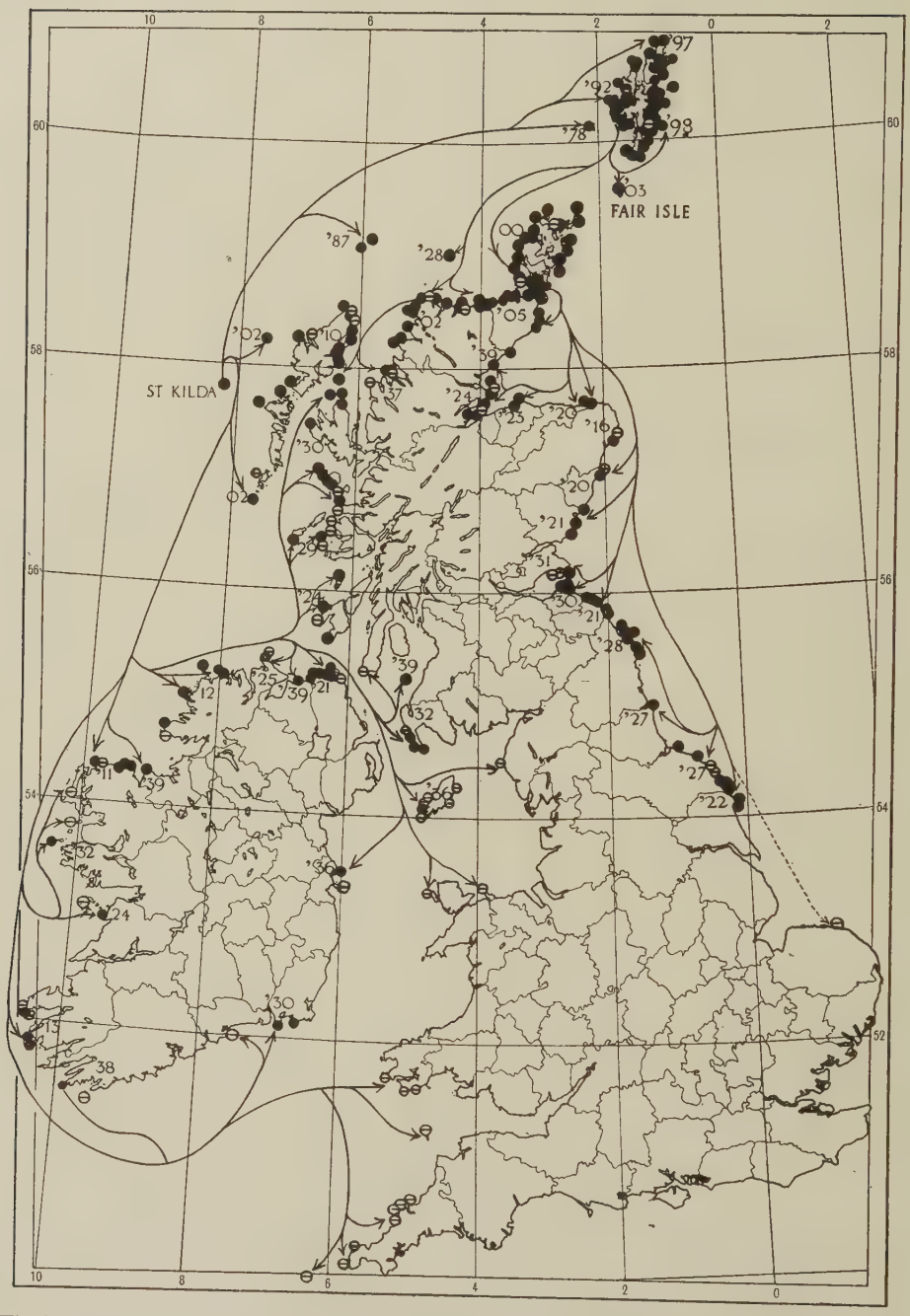


Fig. 7. Map of the British Isles showing the main directions of spread, on the hypothesis that the spread originated from St Kilda. The dotted line traces the spread to Norfolk, where fulmars were found to be prospecting sites in 1940. While outside the period of the inquiry, this is included because of its interest.

(3) *South-westwards and then east.* The spread in the Barra Head direction continued after a 9-year interval, to the north-west coast of Mayo, Eire, which was reached in 1911. The Donegal coast was colonized in the following year. In 1913 the Kerry coast was reached; after this the birds spread inwards to Clare (1924) and Galway (1932), and rounded the south coast of Ireland to reach Wexford in 1930. Birds first bred on the intermediate coast of Cork in 1938. It can be imagined that it is a continuation of this trend that has brought them across to Pembrokeshire, Lundy Island (north Devon), Cornwall and the Scillies, in each of which districts they are now present but have not yet been proved to breed, and to Ushant, north-west France, where (see p. 240) they were prospecting in 1935.

(4) *Southwards.* A continuation eastwards and then south from west Donegal seems to have brought the birds to Antrim by 1921. The fulmar bred first on the cliffs of east Donegal in 1925, and for the first time in Derry in 1939. The Mull of Galloway was reached in 1932, the Isle of Man and Lambay Island (Dublin) in 1936, and colonies (but not breeding colonies) were present in 1939 at St Abb's Head (Cumberland), Gt Orme's Head (Carnarvon) and Holyhead.

(5) *Northwards.* A probable branch of the trend described above brought the birds from the south to Islay in 1924, the mid-group of the Inner Hebrides in 1929, and Skye in 1930. This interesting trend, which appears to have taken place in the opposite direction from the other ones, seems to have now merged with the general eastward trend (2) into the Minch. The second stage of most trends—the colonization of the less oceanic coasts—is exemplified in this case by the colonization of Ailsa Craig (Clyde) in 1939, and the existence of a (probably non-breeding) colony on the Mull of Kintyre.

(*b*) *The population*

One of the original objects of the inquiry was to make a study of the present population of the fulmar. It was soon found that the actual number of pairs breeding in a colony at any one time was extremely hard to assess from the published or communicated information. It was, however, found practicable to assign the population of colonies to the logarithmic orders described on pp. 209–10, and, as can be seen from the treatment in § 3, to follow the population changes (under these headings) historically.

(1) In order to follow the population as a whole throughout the years, a chart was prepared (a copy of which is deposited at the Edward Grey Institute) on which the population of each colony in each year since 1874, or since its foundation, was shown by interpolation. This interpolation was made under the following rules:

(*a*) The first *recorded* breeding year was taken as the first year of breeding; thus a colony like Northwall, Orkney, recorded as 0:1918, 1:1926 was considered to be of Order 0 up to 1925.

(*b*) Birds at a colony were held to continue, from year to year, in the order last recorded, unless there was evidence of change. Thus Pennan Head, Aberdeen, last recorded in 1920 as Order 2, was held to be of Order 2 in 1939.

(*c*) A colony recorded as breeding in one year in one order, and in another year in the next order, and there being no evidence on the status in between the two years (the orders being 1 or higher) was held to change from one order to another exactly between the two years. If the number of intervening years was odd, then the population in the middle year was held to be of the lower order. Thus the Shiants, Outer Hebrides, recorded as Order 1 in 1910, and Order 2 in 1926 (there being no intermediate record) were considered to be of Order 1 until 1918, and of Order 2 from 1917.

(*d*) A colony recorded as breeding in one year in one order, and in another year in another order not the next (otherwise as in (*c*)), was assigned to appropriate orders during the intervening years by sharing those years equally between the orders concerned. Thus Sula Sgeir, Outer Hebrides, recorded as Order 1 in 1887, and as Order 3 in 1932 (there being no intermediate record) was considered to be of Order 1 until 1902, of Order 2 from 1903 to 1916, and of Order 3 from 1917.

Using the values *interpolated* under these rules, it is possible to construct a table showing the population (under the appropriate 'orders') of each vice-county in every fifth year (Table 3). This table has been used in the construction of Figs. 1, 2, 10 and 11. With the exception of the two colonies in Order 5, it was found (by investigating the colonies whose *actual* population was known) that the *mean* population of all colonies in order n was approximately $4 \times 10^{n-1}$; to take an example, of the 28 colonies in 1939 in Order 3, each probably had, on an average, 4×10^2, i.e. 400 pairs of breeding birds. The two Order 5 colonies are St Kilda and Foula; the population of the former is dealt with in later discussion (p. 237) and that of the latter has been observed, during recent years, to be about 10,000 breeding pairs. On this basis, using Table 3, the population of each vice-county has been tabulated for each fifth year since 1874 (Table 4) (excluding that of St Kilda). The consequence of using $4 \times 10^{n-1}$ for the population of a colony in Order n, has been the appearance of such figures as 17,668 pairs for the population of Shetland in 1934. Accuracy of such a kind could never, of course, be claimed, but the figures stand in order that the year total for the British Isles, and the logarithmic order into which each vice-county population falls, can be established. Fig. 8 is an 'arithlog' graph of the population outside St Kilda since 1874, based on Table 4: it indicates the spread of the population in time.

(2) From Table 4 a series of maps (Fig. 9) has been constructed to show the spread in both space and time of the population. These maps indicate the directions of the spread. They show, too, how the population is to-day still numerically concentrated almost entirely in the north: in fact, that the fulmar's numerical distribution does not correspond to its spatial distribution. Since consideration of distribution in time of number of colonies in each 'order' might prove useful in investigating the nature of the spread, Fig. 10 and Table 5 have been constructed from Table 3; and Fig. 11 from Table 5. From examination of Figs. 10 and 11 it can be seen that, of the total number

Table 3. *The number of colonies in each order per vice-county in each fifth year since* 1874

Province	Vice-county	No.	1874 Order 0	1	2	3	4	5	1879 0	1	2	3	4	5	1884 0	1	2	3	4	5	1889 0	1	2	3	4	5	1894 0	1	2	3
N. Highlands	W. Sutherland	108	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Caithness	109	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
N.W. Isles	N.W. Isles	110	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	1	.	2	.	.	.	1	.	2	.	.
N. Isles	Orkney	111	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Shetland	112	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	1	1	1	.
	Total		.	.	.	.	.	1	.	.	1	.	.	1	.	.	1	.	.	1	.	2	1	.	.	1	1	3	1	.
Total breeding-colonies						1						2						2						4						5
Total colonies					1						2						2						4						6	

Province	Vice-county	No.	1909 Order 0	1	2	3	4	5	1914 0	1	2	3	4	5	1919 0	1	2	3	4	5	1924 0	1	2	3	4	5	1929 0	1	2	3
Peninsula	W. Cornwall	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	E. Cornwall	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	N. Devon	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anglia	E. Norfolk	27	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
S. Wales	Pembroke	45	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
N. Wales	Carnarvon	49	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Anglesey	52	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Humber	S.E. Yorks	61	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.
	N.E. Yorks	62	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	1	2	.	.	.
Tyne	Durham	66	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
	Cheviot	68	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	2	.	.	.	.	.	3	2	.	.	.
Lakes	Cumberland	70	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Isle of Man	71	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
W. Lowlands	Wigtownshire	74	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
E. Lowlands	Berwick	81	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	2	.	.	.	.	1	2	.	.	.
	E. Lothian	82	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	2	.	.	.	.
E. Highlands	Fife	85	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.
	Angus	90	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	1	.	.	.
	Kincardineshire	91	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	1	1	.	.	.	.	1	1	.	.	.
	N. Aberdeenshire	93	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	1	.	.
	Banff	94	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.
	Morayshire	95	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	1	1	.	.
W. Highlands	Westerness	97	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Clyde Islands	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Cantire	101	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
	Ebudes South	102	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	1	2	.	.	.
	Ebudes Mid	103	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.
	Ebudes North	104	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
N. Highlands	W. Ross	105	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	E. Ross	106	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	2	1	.	.	.	.	4	1	.	.	.
	E. Sutherland	107	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	W. Sutherland	108	.	2	1	.	.	.	1	3	2	.	.	.	1	4	2	.	.	.	1	4	2	.	.	.	2	3	1	2	.
	Caithness	109	1	.	1	.	.	.	3	.	2	.	.	.	3	1	2	.	.	.	2	1	2	2	.	.	1	1	2	3	.
N.W. Isles	N.W. Isles	110	.	1	3	.	.	1	2	2	3	1	.	1	2	1	4	2	.	1	2	1	4	2	.	1	2	2	3	3	.
N. Isles	Orkney	111	2	1	2	.	.	.	3	8	1	1	.	.	4	10	3	1	.	.	5	8	6	1	.	.	6	8	6	3	.
	Shetland	112	6	10	6	.	1	.	5	16	8	1	1	.	6	14	10	1	1	.	6	17	8	3	1	.	5	15	11	5	.
Ireland	Kerry	113	.	.	.	.	.	.	.	.	1	.	.	.	1	.	1	.	.	.	1	.	.	1	.	.	1	.	.	1	.
	Cork	115	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Waterford	118	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Clare	121	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.
	Wexford	124	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
	Galway	128	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Dublin	133	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	W. Mayo	139	1	.	.	.	.	.	.	1	1	.	.	.	.	1	1	.	.	.	1	1	1	.	.	.	2	1	1	.	.
	Sligo	140	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	E. Donegal	146	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.
	W. Donegal	147	1	.	.	.	.	.	1	.	1	.	.	.	1	.	1	.	.	.	.	1	1	.	.	.	.	1	1	.	.
	Antrim	151	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	1	.	.
	Derry	152	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Total		11	14	13	.	1	1	17	30	19	3	1	1	26	31	25	4	1	1	31	44	25	9	1	1	39	50	29	17	.
Total breeding colonies						29						54						62						80						98
Total colonies					40						71						88						111						137	

1899					1904						
1	2	3	4	5	0	1	2	3	4	5	
											No.
.	.	.	.	.	.	3	.	.	.	.	108
.	.	.	.	.	1	.	.	.	.	.	109
2	.	.	.	1	.	2	2	.	.	1	110
.	.	.	.	.	1	1	1	.	.	.	111
5	1	1	.	.	2	7	2	1	.	.	112
7	1	1	.	1	4	13	5	1	.	1	—
			10					20			
		14					24				

1934					1939						
1	2	3	4	5	0	1	2	3	4	5	
											No.
.	.	.	.	.	6	.	.	.	.	.	1
.	.	.	.	.	1	.	.	.	.	.	2
.	.	.	.	.	1	.	.	.	.	.	4
.	.	.	.	.	.	.	.	.	.	.	27
.	.	.	.	.	3	.	.	.	.	.	45
.	.	.	.	.	1	.	.	.	.	.	49
.	.	.	.	.	1	.	.	.	.	.	52
.	1	.	.	.	.	1	2	.	.	.	61
1	1	.	.	.	2	3	1	.	.	.	62
.	1	.	.	.	.	.	1	.	.	.	66
4	.	.	.	.	.	5	1	.	.	.	68
.	.	.	.	.	1	.	.	.	.	.	70
.	.	.	.	.	5	1	.	.	.	.	71
1	.	.	.	.	1	1	2	.	.	.	74
2	2	.	.	.	.	3	2	.	.	.	81
.	.	.	.	.	.	2	1	.	.	.	82
1	.	.	.	.	2	1	.	.	.	.	85
.	.	.	.	.	.	2	.	.	.	.	90
2	.	.	.	.	1	2	.	.	.	.	91
.	1	.	.	.	1	1	1	.	.	.	93
.	1	.	.	.	.	.	1	.	.	.	94
.	1	.	.	.	.	1	1	.	.	.	95
.	.	.	.	.	1	.	.	.	.	.	97
.	.	.	.	.	.	1	.	.	.	.	100
.	.	.	.	.	1	.	.	.	.	.	101
2	1	.	.	.	1	1	2	.	.	.	102
.	2	.	.	.	3	.	1	1	.	.	103
.	.	.	.	.	1	6	3	.	.	.	104
.	.	.	.	.	2	.	1	.	.	.	105
.	.	.	.	.	2	5	.	.	.	.	106
.	.	.	.	.	.	1	.	.	.	.	107
.	2	2	.	.	2	2	8	4	.	.	108
.	3	3	.	.	.	3	4	4	.	.	109
.	1	5	.	1	4	7	4	5	1	1	110
.	8	3	.	.	2	13	5	5	1	.	111
.	10	8	1	1	2	26	18	8	2	1	112
.	.	1	.	.	2	1	1	1	.	.	113
.	.	.	.	.	3	.	1	.	.	.	115
.	.	.	.	.	1	.	.	.	.	.	118
.	.	.	.	.	.	1	.	.	.	.	121
.	.	.	.	.	.	1	1	.	.	.	124
1	.	.	.	.	1	.	1	.	.	.	128
.	.	.	.	.	1	.	1	.	.	.	133
2	.	.	.	.	3	1	3	.	.	.	139
.	.	.	.	.	.	.	1	.	.	.	140
.	.	.	.	.	1	.	1	.	.	.	146
2	.	.	.	.	1	2	4	.	.	.	147
3	.	.	.	.	1	3	3	.	.	.	151
.	.	.	.	.	.	1	.	.	.	.	152
43	22	1	2		61	98	76	28	4	2	
		139						208			
195											
						269					

Table 4. *Breeding pair population of Britain's vice-counties (excluding St Kilda) for each fifth year since* 1874
(*see* p. 230 *for discussion of accuracy of figures*)

Province	Vice-county	No.	1874	1879	1884	1889	1894	1899	1904	1909	1914	1919	1924	1929	1934	1939	No.
Peninsula	W. Cornwall	1	—	—	—	—	—	—	—	—	—	—	—	—	—	0	1
	E. Cornwall	2	—	—	—	—	—	—	—	—	—	—	—	—	—	0	2
	N. Devon	4	—	—	—	—	—	—	—	—	—	—	—	—	—	0	4
S. Wales	Pembroke	45	—	—	—	—	—	—	—	—	—	—	—	—	0	0	45
N. Wales	Carnarvon	49	—	—	—	—	—	—	—	—	—	—	—	—	—	0	49
	Anglesey	52	—	—	—	—	—	—	—	—	—	—	—	—	—	0	52
Humber	S.E. Yorkshire	61	—	—	—	—	—	—	—	—	—	0	4	40	40	84	61
	N.E. Yorkshire	62	—	—	—	—	—	—	—	—	—	—	0	8	44	52	62
Tyne	Durham	66	—	—	—	—	—	—	—	—	—	—	—	4	40	40	66
	Cheviot	68	—	—	—	—	—	—	—	—	—	0	0	8	16	60	68
Lakes	Cumberland	70	—	—	—	—	—	—	—	—	—	—	—	—	—	0	70
	Isle of Man	71	—	—	—	—	—	—	—	—	—	—	—	—	0	4	71
W. Lowlands	Wigtownshire	74	—	—	—	—	—	—	—	—	—	—	—	0	4	84	74
E. Lowlands	Berwickshire	81	—	—	—	—	—	—	—	—	—	0	8	8	88	92	81
	E. Lothian	82	—	—	—	—	—	—	—	—	—	—	0	0	4	48	82
E. Highlands	Fife	85	—	—	—	—	—	—	—	—	—	—	0	0	4	4	85
	Angus	90	—	—	—	—	—	—	—	—	—	—	4	4	4	8	90
	Kincardine	91	—	—	—	—	—	—	—	—	0	0	4	4	8	8	91
	N. Aberdeen	93	—	—	—	—	—	—	—	—	0	40	40	40	44	44	93
	Banff	94	—	—	—	—	—	—	—	—	—	0	4	4	40	40	94
	Morayshire	95	—	—	—	—	—	—	—	—	—	0	4	44	44	44	95
W. Highlands	Westerness	97	—	—	—	—	—	—	—	—	—	—	—	—	0	0	97
	Clyde Islands	100	—	—	—	—	—	—	—	—	—	—	—	—	—	4	100
	Cantire	101	—	—	—	—	—	—	—	—	—	—	—	0	0	0	101
	Ebudes South	102	—	—	—	—	—	—	—	—	—	—	4	8	48	84	102
	Ebudes Mid	103	—	—	—	—	—	—	—	—	—	—	—	8	80	440	103
	Ebudes North	104	—	—	—	—	—	—	—	—	—	—	—	0	16	144	104
N. Highlands	W. Ross	105	—	—	—	—	—	—	—	—	—	—	—	—	0	40	105
	E. Ross	106	—	—	—	—	—	—	—	—	—	0	4	4	16	20	106
	E. Sutherland	107	—	—	—	—	—	—	—	—	—	—	—	—	—	4	107
	W. Sutherland	108	—	—	—	—	—	0	12	48	92	96	96	852	900	1,928	108
	Caithness	109	—	—	—	—	—	—	0	40	80	84	884	1,284	1,324	1,772	109
N.W. Isles	N.W. Isles	110	—	—	—	8	8	8	88	124	528	964	964	1,328	2,060	6,188	110
N. Isles	Orkney	111	—	—	—	—	—	0	44	84	472	560	672	1,472	1,568	6,252	111
	Shetland	112	—	40	40	40	44	460	508	4,280	4,784	4,856	5,588	12,500	17,668	22,024	112
Ireland	Kerry	113	—	—	—	—	—	—	—	—	40	40	400	400	404	444	113
	Cork	115	—	—	—	—	—	—	—	—	—	—	—	—	—	40	115
	Waterford	118	—	—	—	—	—	—	—	—	—	—	—	—	0	0	118
	Clare	121	—	—	—	—	—	—	—	—	—	—	4	4	4	4	121
	Wexford	124	—	—	—	—	—	—	—	—	—	—	—	0	0	44	124
	Galway	128	—	—	—	—	—	—	—	—	—	—	—	—	40	40	128
	Dublin	133	—	—	—	—	—	—	—	—	—	—	—	—	—	40	133
	W. Mayo	139	—	—	—	—	—	—	—	0	44	44	44	44	80	124	139
	Sligo	140	—	—	—	—	—	—	—	—	—	—	—	—	—	40	140
	E. Donegal	146	—	—	—	—	—	—	—	—	—	0	0	4	4	40	146
	W. Donegal	147	—	—	—	—	—	—	—	0	40	40	44	44	84	168	147
	Antrim	151	—	—	—	—	—	—	—	—	—	—	4	44	128	132	151
	Derry	152	—	—	—	—	—	—	—	—	—	—	—	—	—	4	152
	Totals	48	—	40	40	48	52	468	652	4,576	6,080	6,724	8,776	18,160	24,804	40,632	48

Table 5. *Number of colonies in each different order expressed as a percentage of the whole number in each fifth year since* 1874

	Orders				
Year	0	1	2	3	4 and 5
1874	—	—	—	—	100
1879	—	—	50·0	—	50·0
1884	—	—	50·0	—	50·0
1889	—	50·0	25·0	—	25·0
1894	16·7	50·0	16·7	—	16·7
1899	28·6	50·0	7·1	7·1	7·1
1904	16·7	54·2	20·8	4·2	4·2
1909	27·5	35·0	32·5	—	5·0
1914	24·0	42·3	26·7	4·2	2·8
1919	29·5	35·2	28·4	4·5	2·3
1924	27·9	39·7	22·5	8·1	1·8
1929	28·5	36·5	21·2	12·4	1·5
1934	28·7	36·5	22·1	11·3	1·5
1939	22·7	36·4	28·3	10·4	2·2

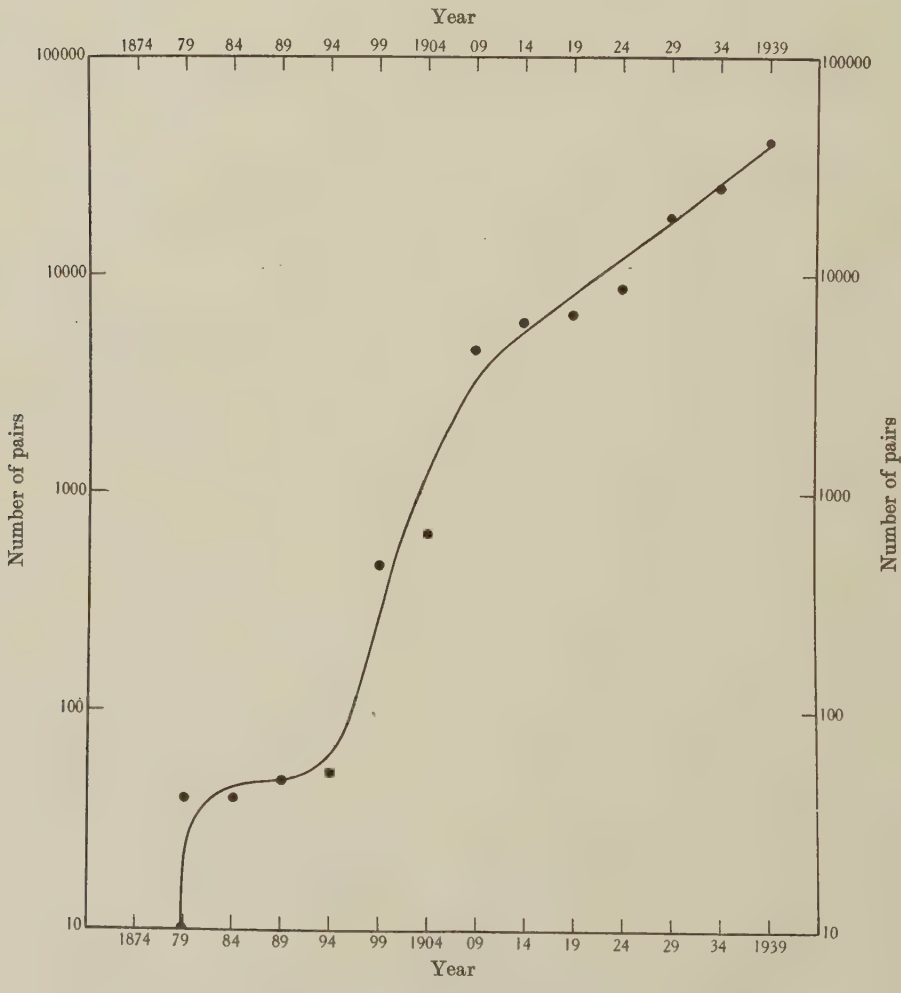


Fig. 8. Number of pairs breeding in the British Isles outside St Kilda in each fifth year since 1874.

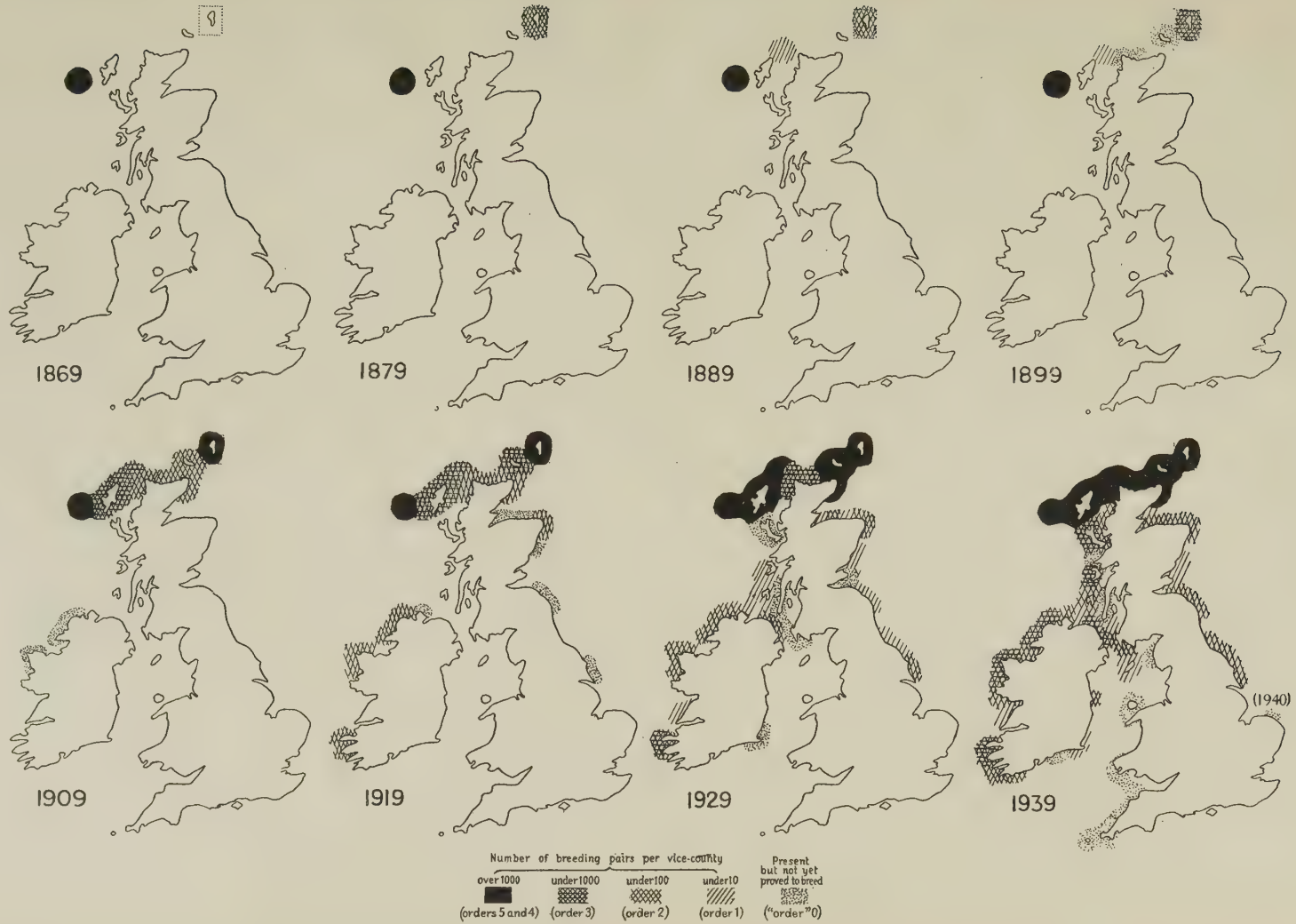


Fig. 9. Series of eight maps showing the spread in Britain in space, time (10-year intervals) and population.

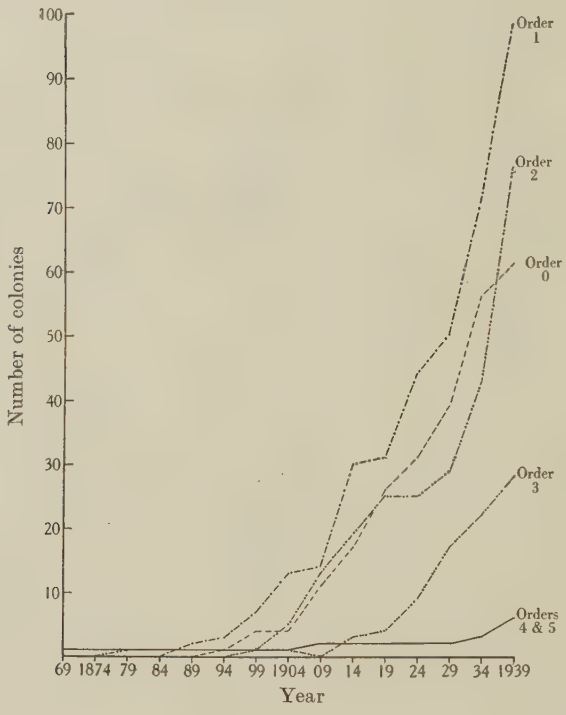


Fig. 10. Number of the colonies of the different orders at five-yearly intervals.

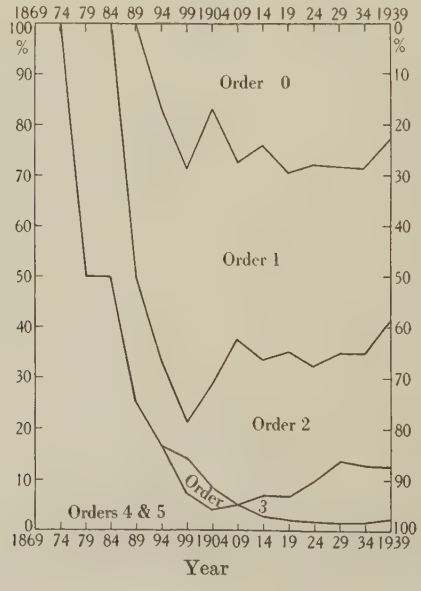


Fig. 11. Numbers of the colonies of different orders represented as percentages of the total number of colonies in each fifth year since 1874.

of colonies, those in Order 1 have constituted the greatest fraction ever since 1889, and since 1909 have never failed to be between 35·0 and 42·3 % of the whole number. From 1909 until 1934 the percentage of the total number lying in Order 0 has also been remarkably constant, not being higher than 29·5 % or lower than 24·0 %. In 1939, however, this percentage dropped to 22·7, and Fig. 10 lends further weight to the suspicion that the amount of prospecting of new colonies by the fulmar is now slightly falling off. In 1939, too, the percentage in Order 2 jumped from 22·1 to 28·3, having been close to the first of these figures in 1924, 1929, and 1934; and since 1924 there has been a tendency for the fraction of the total number of colonies represented by those in Orders 3, 4 and 5 to increase slowly. Hence it is clear that the occupation of new colonies continues at present at a somewhat slower rate than previously, and that the main increase in population is coming from the growth of existing colonies, a growth which is continually tending to raise them to higher orders.

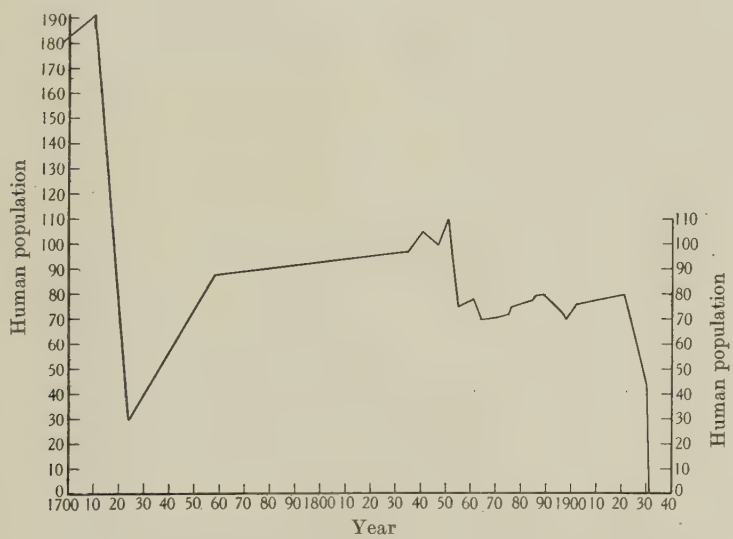


Fig. 12. The changes in the human population of St Kilda since 1697.

(c) *St Kilda and the spread*

St Kilda has always interested observers of various kinds, and the books and other literature about this remote group of islands are remarkably numerous. Stewart's (**711**) bibliography gives a list of such publications. Such of the history of St Kilda as concerns this inquiry is set out on pp. 216–19. From this information it has been possible to prepare a chart (Fig. 12) of the changes in the human population of St Kilda since Martin Martin's (**486**) visit in 1697. It can be seen from the collected information (p. 236) that the taking of young fulmars by the inhabitants of St Kilda went on long after the

spread of the bird to other parts of Britain began. Most of those who have argued about the cause of the fulmar's spread have ascribed it to the overflow from St Kilda consequent upon the neglect of the bird as a source of food supply by the inhabitants, as soon as preserved food became available to them. This argument is summarized by MacGregor (**463**). It should be mentioned that the first regular steamship service to the islands started in 1877. Ritchie's paper (**622**) on this subject stresses the possible importance of this factor, as does that of Gordon (**295**).

After studying the literature exhaustively, it is our conclusion that the arrival of regular food supplies from the mainland made very little difference to the number of fulmars, *in proportion to the human population*, that were killed for food and oil. Let us consider Table 6.

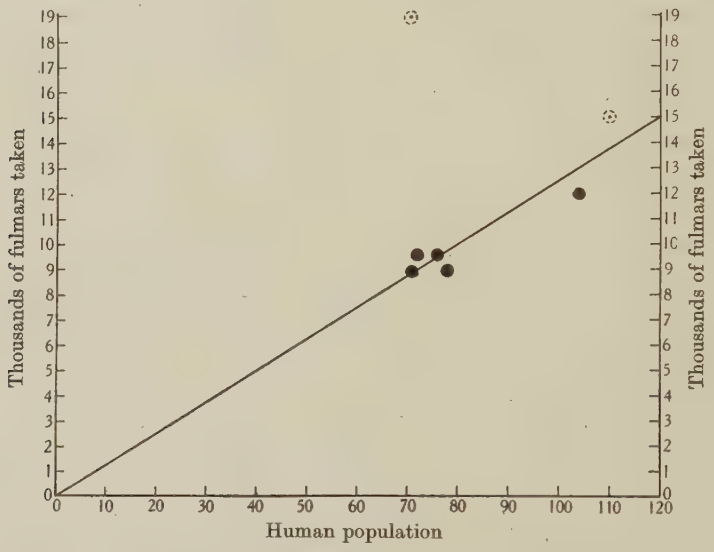


Fig. 13. Number of young fulmars taken, against human population.

Table 6

Year	Human population (by interpolation, when necessary)	No. of young killed annually
1840	104	12,000 on estimate
(1851	110	15,000; not direct observation)
1871	71	19,000 (prob. exaggerated)
1875	72	*c.* 9600
1889	80	800 a day
1897	71	8960
1898	70	'Not caught in any numbers'
1902	76	9600
1910	78	9000

From this table, Fig. 13 showing the relation between the human population and the numbers taken, has been constructed. This, with Fig. 12 and Table 4, has been used to construct Table 7. Clearly, though the number of

fulmars taken in proportion to the human population in years after 1877 may have fluctuated (vide 1898) the tradition of taking them was still maintained, at least until 1910, and the numbers taken in proportion to the human population remained in the long run very much the same.

Table 7. (Figures approximate.)

This has been used to construct Fig. 14.

Year	Human population St Kilda	No. of young taken on St Kilda	No. of young surviving on St Kilda	No. of young produced outside St Kilda	Total no. of young produced
1874	72	9,000	12,000	0	12,000
1879	76	9,600	11,400	40	11,440
1884	78	9,800	11,200	40	11,240
1889	80	10,000	11,000	48	11,048
1894	74	9,300	11,700	52	11,752
1899	71	8,900	12,100	468	12,568
1904	76	9,600	11,400	652	12,052
1909	77	9,700	11,300	4,576	15,876
1914	79	9,900	11,100	6,080	17,180
1919	80	10,000	11,000	6,724	17,724
1924	67	8,400	12,600	8,776	21,376
1929	47	5,900	15,100	18,160	33,260
1934	0	0	21,000	24,804	45,804
1939	0	0	21,000	40,092	61,092

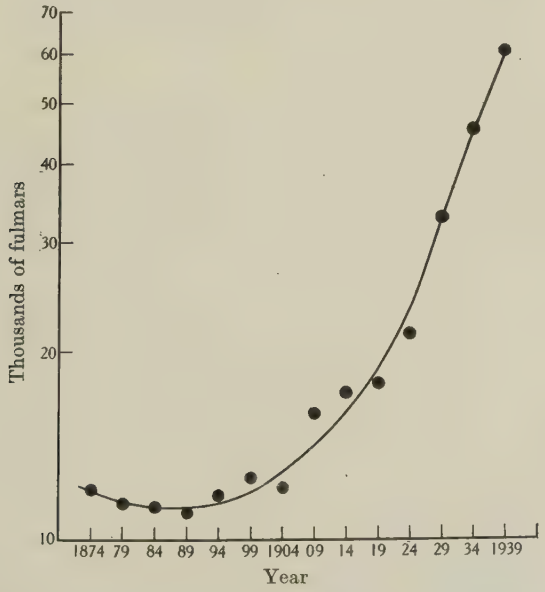


Fig. 14. Total number of young fulmars produced in Britain each fifth year since 1874. (See this page for assumptions.)

The figures for the total number of young produced in Britain are based on the following assumptions:

(1) That the number of breeding pairs on St Kilda has been permanently 21,000. This, of course, is only a generalized figure, and does not allow for the fluctuations which at one time or another have almost certainly occurred (see

remarks on pp. 217–18 under 1877, 1886, 1900, 1903, 1914, 1931, and 1939). The figure of 21,000 is based on the 1939 count. (2) That those young fulmars not taken on St Kilda survive to fly. (3) That no young fulmars are taken outside St Kilda. We have no evidence that any colony is raided in order to get young birds for human food, with the possible exception of that on Sula Sgeir, which is raided almost annually for gannets, and where a few fulmars may be taken. (4) That each breeding pair outside St Kilda, as set out in Table 4, produces one young. Though two eggs are quite often laid in Iceland (**435**), cases of this on Sula Sgeir in 1939 (**848**) and on Sanday, Orkney, in 1934 are the only ones we know of in Britain.

We can now draw the following conclusions from our study of St Kilda.

(*a*) There is no evidence that the supplying of the St Kildans with preserved foodstuffs since 1877 caused them to alter the quality, or even the quantity of their traditional bird-killing habits.

(*b*) If changes in the St Kilda fulmar population are at all responsible for the colonization of stations in other parts of Britain, and if these changes have anything to do with human population, they must be the result of changes in the number rather than in the habits of the human population.

(*c*) Such a change might well be the sudden drop in the human population from 110 in 1851 to 70 in 1864, due to migration to Australia and to drowning (see Fig. 12).

(*d*) This change, it may be remarked, took place at a time when the St Kildans were in a particularly indigent and demoralized state, and preceded by a decade the arrival of a regular steamship service (a service which was a partial result of public feeling with regard to the condition of the St Kildans).

(*e*) The temptation to connect the Industrial Revolution with the spread of the fulmar, fascinating from an ecological point of view, can now be indulged. It can be concluded that its more direct product, preserved foodstuffs, is probably not responsible; but its indirect product, the reduction of markets for the simple and primitive merchandise (wool, tweeds, and other sheep products) of the St Kildans, which led to a reduction in their population by migration, may have been partly responsible.

Such is the effect the situation in St Kilda may have had on the fulmar population of Britain. The question arises, is this the sole cause of the remarkable changes which have taken place? The answer to this can be partly found by a study of the distribution of the fulmar abroad.

(*d*) *The fulmar abroad*

Changes in the distribution of the fulmar in historical times are known to have taken place also in Iceland, the Faeroes, Norway, and France.

(1) *Iceland.* Here the fulmar has a very wide distribution. Up to 150,000 have been killed in certain years. It breeds almost all round the coast, but mostly in the Mýrdalsfjall district, under Eyjafjall, in the Westmann

7

Photos 4–7. Fowling on St. Kilda. (4) Fanciful picture (not from life) from MacPherson (**470**). Note the incorrect standing position of the fulmars. (5) Noose, from J. H. Gurney ("The Gannet" ... London, 1913). (6) Noose attached to stick, from MacPherson. (7) Fowling scene drawn from life (1898), from Heathcote (**360**).

4 5 6

Islands, Krísuvík, Hafnaberg,[1] Myrar, Látrabjarg, Drangey, Grímsey, Svörtuloft, Hornströnd and Húsavík. In the Westmann Islands about 20,000 young were taken in 1821, 20,000–30,000 around 1852, 24,229 in 1898 (apparently a bad season, for at this time 30,000 were taken in a good year), and certainly 20,000 a year up to about 1920. At Grímsey huge numbers have bred for many years; recently 3000–4000 have been taken in some years. In 1931 2620 were taken. In 1935 an earthquake destroyed about 95 % of the eggs. Most interesting of all, in the Mýrdalsfjall district the birds arrived at Höfðubrekkuháls in about 1820, and in Hjörleifshöfði in 1836. By 1936 they were in all Mýrdalsfjall, and 20,000–25,000 young birds were being taken every year. (**18**, **60**, **197**, **254**, **332**, **368**, **404**, **412**, **525**, **655**, **732**, **964**.)

(2) *The Faeroes.* Here the fulmar arrived sometime between 1816 and 1839 (in 1800 it was only known as a visitor to the surrounding seas), and by 1900 was breeding in nearly all the islands. The history of the bird in some of these is worth discussing. *Suderø.* Birds arrived here near Quelbø between 1816 and 1839; 3 eggs were taken in or before 1856. By 1872 they were abundant. *Skuø.* Birds may have arrived in about 1845, and were certainly breeding by 1849. 3300 young were killed in 1937. *Little Dimon.* Fulmars may have arrived in about 1845, and were certainly breeding in 1905. *Store Dimon.* The early history of the fulmar here was the same as on Skuø. 10 eggs were taken on 30 June 1849. Between 1866 and 1896 it had increased from a few to 5000–6000 pairs. In 1883 1000 young were taken and in the last decade about 80,000 (more than Britain's present annual production) have been killed annually. *Sandø.* Fulmars were possibly breeding here by 1849. *Troldhoved* (*off Sandø*). Fulmars arrived here in about 1859. *Hestur.* Birds were breeding on the eastern side and on the Alvastakkur in 1936. *Myggenaes Holm.* Birds arrived here in about 1860, and were breeding in large numbers by 1872. In 1883, 1100 young were taken, and in 1891, 3000. *Vaagø.* Fulmars arrived in about 1865. *Strømø.* Near Sydradalur many were nesting in 1936. *Fuglø and Viderø.* Birds were breeding here in large numbers by 1872. *Nolsø.* Birds arrived in about 1892, and many were present, some breeding, in 1897, 1898, 1899, 1900, 1901 (300 pairs on 2 March on the east side), 1902, 1905, and onwards, steadily increasing. We must discard the account that the resentment expressed by the King's Sheriff, respecting a bird that had established itself in about 1728 on Myggenaes Holm and on Sandø, was directed against the fulmar.

Resentment, however, is directed against the fulmar to-day, and the taking of young is now prohibited. The reason is that an outbreak of psittacosis has been traced to the young fulmars, which, when captured at the end of August and the beginning of September, are split and salted mainly by the women of the islands. Of 165 cases (some fatal) between 1933 and 1937 only 24 were

[1] Mentioned by Faber (**254**), but not found there by Newton (**525**) in 1858; in 1939 none was seen breeding on mainland or islands (**964**).

men, since, owing to this task, the women are much more liable to infection. This outbreak did not occur until the fulmars had reached a high population, and although psittacosis affects the young fulmars themselves it would probably have passed unnoticed were it not for its effect on human beings. The stopping by law of fulmar-taking—and over 100,000 young ones were being captured in recent years—is likely to have an important effect on the population of the fulmar in the future. (**1**, **7**, **8**, **9**, **10**, **11**, **12**, **13**, **132**, **257**, **421**, **440**, **527**, **558**, **559**, **657**, **764**, **790**, **798**; psittacosis: **20**, **63**, **330**, **331**, **587**, **601**.)

(3) *Norway.* In 1924 the fulmar was found breeding for the first time in Norway on the island of Rundø, midway between Aalesund and Stat. Birds may have been present in the breeding season since about 1914, and were certainly so in 1921. In 1924, when breeding was first proved, about 100 pairs were present round the island in all. In 1926 there were about 45 breeding pairs, in three or four different places.

0:1914–21, 2:1924–26. (**19**, **390**, **449**, **873**.)

(4) *France.* Until recently, the fulmar was regarded as a 'very accidental' visitor to the north and west coasts of France. In 1935, however, birds turned up near the lighthouse at Ushant in the breeding season. On 26 April 4 were seen, on 29 April the birds were still there but there was no sign of breeding, and on 30 April the birds were not seen.

0:1935. (**544**, **905**.)

We may now be permitted further conclusions.

(*a*) Spread of the same kind as in Britain has been a feature of the history of the fulmar in Iceland, the Faeroes, Norway and France in the last 120 years. (*b*) The spreads in Iceland and to the Faeroes are phenomena with no causes obviously traceable to human agency; or, in particular, to a change in human feeding habits; the opposite is, in fact, the case, for the eating of fulmars by man has resulted from the birds' arrival and spread. (*c*) The birds that arrived in Norway in about 1914 and in France in 1935 are likely to have been derived from the British (or possibly in the former case, the Faeroe) spread.

We can claim, in fact, that the spread of the fulmar in the North Atlantic is certainly due to deeper biological causes than to its interrelation with man on St Kilda, though undoubtedly the latter has had a serious but secondary effect on the British population. We are not the first to make such a suggestion, as Wiglesworth (**784**) has already pointed out the inadequacy of the 'St Kilda theory'.

(*e*) *Some mathematical considerations*

The steepest point of the curve in Fig. 14 falls in about 1927, and at this point it can be found, by direct measurement, that the British population was increasing at the rate of about 7·1 % per annum (multiplying itself by $4\frac{1}{2}$ in 22 years). It has been shown (**271**) that in a species which lays a single egg,

the maximum rate of increase (which depends on a sex ratio of 1:1, and immortality of the birds), is given by

$$p_{n+y} - p_{n+(y-1)} - \tfrac{1}{2}p_n = 0, \qquad (1)$$

supposing that there are p_n pairs of birds in the year n, and that a bird hatched in the year n comes to maturity in the year $n+y$.

Wynne-Edwards (**242**) has shown, from very interesting (though largely circumstantial) evidence, that the fulmar, in common, probably, with other oceanic birds, does not breed every year. He has suggested from a study of the wear of claws,[1] moulting dates, the follicular condition of ovaries and the distribution of the birds' summer population, that apparently only about one bird in three breeds in any one year.

Supposing one fulmar in z breeds every year. Then from (1) we have

$$p_{n+y} - p_{n+y-1} - \frac{1}{2z}\,p_n = 0, \qquad (2)$$

and values of p_n will tend (in the long run) to a geometrical progression whose common ratio is the largest root of

$$x^y - x^{y-1} - \frac{1}{2z} = 0, \quad \text{or} \quad x^{y-1}(x-1) = \frac{1}{2z}.$$

We can now consider the British population. Supposing it is quite self-contained, i.e. that in the period under review (1874–1939) no birds have colonized Britain from outside, or left Britain for outside. If we accept this hypothesis (for the purpose of argument) we can find the maximum value of z for the possible value of y (the value is unlikely to be over 7) during the period of most rapid increase (7·1 % p.a.), when the value of x was 1·071. We then construct a table (Table 8).

Table 8

When	$y=$	1	2	3	4	5	6	7
	$z=$	7·04	6·57	6·16	5·73	5·35	5·00	4·67 (approx.)

From this we can conclude that at a period in the history of the British increase, the fulmar must have bred at least one in seven years—or rather at least one in every seven fulmars must have bred. And if, as may well be, the fulmars do not breed in the year after they are hatched, then they must have bred more often than this. If, for instance, they come to maturity in their seventh year, then they must have bred at least once every $4\frac{2}{3}$ years; or out of fourteen birds, at least three must have bred. So if we take Wynne-Edwards's figure of one in three as the normal for the breeding population of fulmars,

[1] Wynne-Edwards's argument from relative claw-wear seems to be based on the supposition that fulmars encounter rock as the usual thing when breeding. Meinertzhagen (**499**) points out that in Shetland fulmars breed on grassy slopes rather than on rock, and this is widely true of the species all over its range in Britain (see p. 248). On the other hand, fulmars repair to rocks, walls, etc. quite often for the purpose of display.

we can now see a minimum at one in 6 ± 1 (the special case if fulmars were immortal).

Thus (if Wynne-Edwards's figure be correct) fulmars in Britain, at their period of greatest increase, bred twice as often as they would have had to do if immortal. Hence we can set a minimum annual loss by mortality (at all stages) at a figure equal to half the number of offspring produced each year.

To meet this loss fulmars must have a minimum mean length of life of $12+y$ years (if a bird hatched in the year n breeds in the year $n+y$).

5. Some biological attributes of the fulmar

(*a*) *Climatic correlations of the present distribution*

Speaking of Arctic birds, including the fulmar, Seebohm (**674**) pointed out in 1887 that 'for some special reason they do not breed in any locality where the mean temperature for the month of July is as high as 60 degrees'. He concluded that Scotland belonged to the 'Arctic regions' in the month of July.

Fig. 15, which is a map on Polar projection, shows: (1) the known breeding range of both subspecies of *Fulmarus glacialis*. (2) The boundaries of the oceanic summer and winter ranges of *Fulmarus glacialis glacialis*. (3) The landward ends of the boundaries of the oceanic range of *F. g. rodgersii*. (4) The position of the 60° F. July isotherm. It is compiled from the work of the following authorities (excluding those for Britain, the Faeroes, Iceland, Norway, and France and a few others consulted):

Novaya Zemlya to Lonely Island: **27, 283, 293, 505, 533, 562, 563, 580, 666.**

Franz Josef Land: **154, 194, 313, 518, 520, 665.**

Spitsbergen and Bear Island: **37, 69, 127, 155, 191, 192, 218, 236, 237, 238, 287, 354, 355, 366, 393, 407, 408, 444, 479, 481, 508, 514, 526, 527, 528, 539, 640, 645, 665, 719, 774, 800.**

Jan Mayen: **74, 152, 264, 517.**

Greenland and Baffin Land (with negative breeding evidence from *Labrador*): **57, 68, 75, 202, 256, 312, 333, 342, 364, 365, 373, 374, 409, 447, 450, 476, 482, 513, 565, 566, 669, 741, 748, 791.**

North Pacific (Fulmarus glacialis rodgersii): **67, 204, 292, 339, 340, 352, 420, 476, 521, 534, 541, 586, 665, 675, 695, 700, 721.**

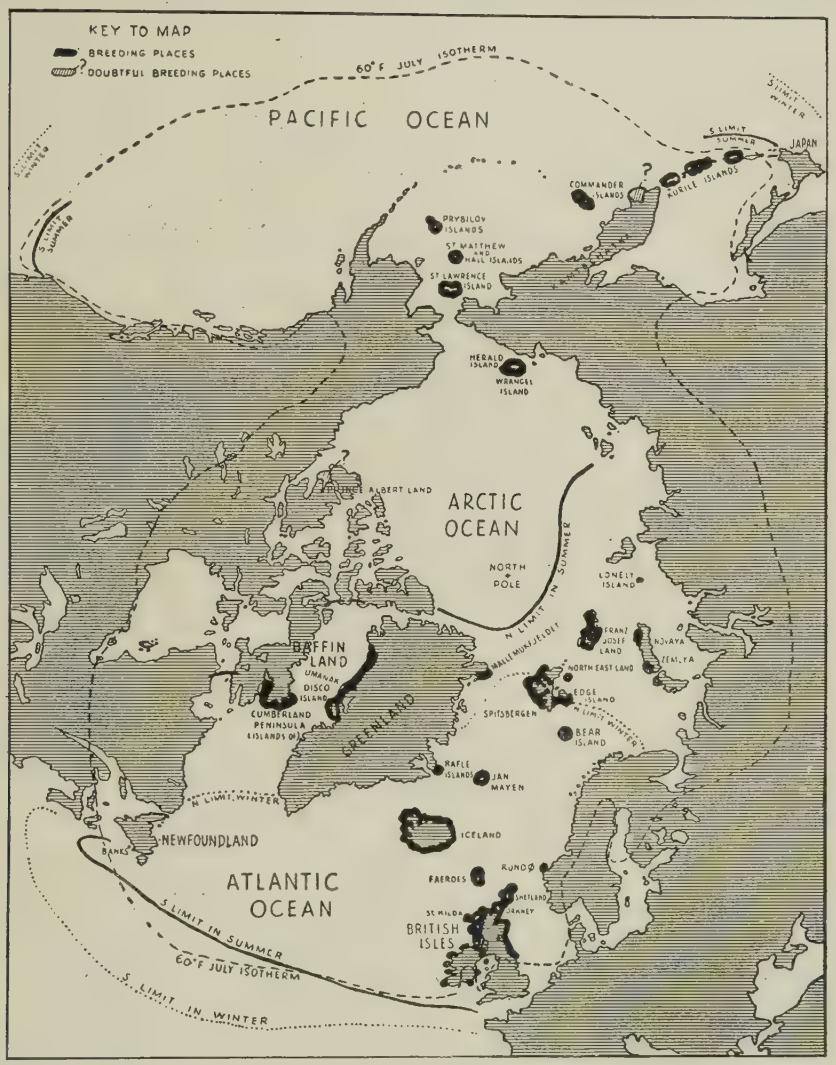
Fulmarus g. glacialis, *southward limit of summer and winter oceanic range*: **241** (references quoted therein also consulted).

Fulmarus g. glacialis, *northward limit of summer and winter oceanic range*: **3, 67, 75, 77, 79, 97, 146, 155, 194, 217, 226, 231, 259, 260, 312, 342, 350, 356, 361, 374, 407, 483, 513, 518, 520, 545, 560, 562, 566, 576, 577, 584, 649, 667, 774, 791.**

From the consideration of Fig. 15 and the previous part of this paper we can reach the following conclusions:

(1) *Fulmarus glacialis* is truly a Palearctic breeding species, with outposts only in such parts of the Nearctic region as have considerable Palearctic affinities (West Greenland, Baffin Island, the Pribilofs). In evolutionary history, it is quite likely to be of European or Asiatic-Arctic origin, and this history must have been an important factor in determining its present distribution. History may be the factor which has determined its absence as a

breeding species from Newfoundland, Labrador, the islands of the Canadian Arctic Archipelago (with the exception of those off the Cumberland Peninsula,



MAP SHOWING WORLD BREEDING-DISTRIBUTION AND OCEANIC RANGE OF THE FULMAR PETREL. BOTH SUBSPECIES ARE SHOWN, *Fulmarus glacialis glacialis* IN THE N. ATLANTIC, AND *F. g. rodgersii* IN THE N. PACIFIC.
(Reproduced from *The Handbook of British Birds* (1940), by permission.)
Fig. 15.

Baffin Island), and the coasts of Alaska and the Aleutian Islands. The world's fulmars have become divided into two populations, which merit subspecific distinction. The typical form, *F. g. glacialis* (L.), breeds in the North Atlantic, occurs eastwards along the Siberian coast as far as the Laptev sea (Lena Delta); and is separated from *F. g. rodgersii* Cassin by the New Siberian Islands,

where no fulmars are found. *F. g. rodgersii* is the North Pacific form which extends through Bering Strait as far west as Wrangell Island.

(2) Such of the fulmar's history as has been under the critical observation of man—the last hundred and twenty years—shows that its population and distribution is in the process of rapid change, at all events in the Iceland-Britain sector.

(3) Its present distribution as a breeding species in the Palearctic region extends, in both Atlantic and Pacific, as far as but no further south than the line represented by the 60° F. July isotherm.

(4) The southern boundary of the July oceanic distribution of the fulmar falls remarkably closely along this isotherm, and penetrates south of it only in the neighbourhood of Cornwall and Ushant (where the bird is seeking to establish itself as a breeding species) and on the Newfoundland Banks.

(*b*) *Breeding habitat selection*

(1) *General topography.* Fulmars appear to have a very clear preference for islands (large and small). They do not breed anywhere on the mainland of the continent of Europe, and probably nowhere on the continent of Asia; and even on the mainland of Britain they are uncommon except on the east side —for instance, none are known to breed on the west mainland of Scotland anywhere between north-west Sutherland and the Mull of Galloway. Such small islands as they choose are practically always oceanic; on large islands and on such mainlands (i.e. *very* large islands like Britain, Iceland, Spitsbergen and Greenland) as they inhabit they breed almost invariably on the most oceanic coasts and headlands. Occasionally they breed at considerable heights, where the cliffs themselves are high, and in Spitsbergen they breed on cliffs and nunataks up to 20 miles inland. Inland breeding in Britain is an interesting but minor recent phenomenon.

Details of breeding and passage at heights and inlands are as follows:

Greenland. Fulmars breed up to 2000 ft. at Ovifak, on Disco Island (**409, 791**).

Spitsbergen. In North-East Land, fulmars cross from Wahlenberg Bay to Extreme Hook; in north-west Spitsbergen they breed at 4000 ft. in Wood Bay; in New Friesland by the Bear Bay glacier, 10 miles inland; in Garwood Land 8–10 miles from the sea up the Ebba Valley, and up to 20 miles from sea and up to 3000 ft. on Mount Terrier and at the head of the Oxford glacier; and in Bünsow Land at some distance from the sea. A 'ceaseless stream' crosses land in summer from Sassen Bay to Stor Fjord. (**37, 287, 354, 393, 444, 508, 539.**)

Bear Island. Fulmars often breed here out of sight of sea; on Miseryfjell and Antarctic-fjellet up to a mile from the coast. (**69, 393.**)

Britain. Table 9 shows, in every tenth year since 1869, the distribution of the colonies according to the heights of the cliffs from sea-level. In the absence of direct information about heights, these have been taken from Bartholomew ½ in., or from Ordnance Survey maps. The actual number of colonies is given, as well as the percentage of the total number, in each height-group. The height-groups are logarithmic, running—under 50, under 100, under 200, under 400, under 800 and under 1600 ft.; heights were taken when possible to the top of what might be taken to be, or what had been observed to be, suitable fulmar breeding ground. From Table 9, Figs. 16 and 17 are constructed. These figures show the general trends of height selection by the fulmar in Britain since the start of its spread.

Table 9. *Distribution of colonies according to height from sea-level*

Year	Type of colony	Total in order	Under 50 ft.		Under 100 ft.		Under 200 ft.		Under 400 ft.		Under 800 ft.		Under 1600 ft.	
			No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1869	Order 5	1	.	.	.	.	.	.	.	.	.	.	1	100·0
	All breeding colonies	1	.	.	.	.	.	.	.	.	.	.	1	100·0
	Total all colonies	1	.	.	.	.	.	.	.	.	.	.	1	100·0
1879	Order 2	1	.	.	.	.	.	.	.	.	.	.	1	100·0
	Orders 3, 4 and 5	1	.	.	.	.	.	.	.	.	.	.	2	100·0
	All breeding colonies	2	.	.	.	.	.	.	.	.	.	.	2	100·0
	Total all colonies	2	.	.	.	.	.	.	.	.	.	.	.	.
1889	Order 1	2	.	.	.	.	1	50·0	1	50·0	.	.	1	100·0
	Order 2	1	.	.	.	.	.	.	.	.	.	.	1	100·0
	Orders 3, 4 and 5	1	.	.	.	.	.	.	.	.	.	.	2	50·0
	All breeding colonies	4	.	.	.	.	1	25·0	1	25·0	.	.	2	50·0
	Total all colonies	4	.	.	.	.	1	25·0	1	25·0	.	.	.	.
1899	Order 0	4	.	.	.	.	.	.	1	25·0	1	25·0	2	50·0
	Order 1	7	.	.	1	14·3	3	42·9	1	14·3	2	28·6	.	.
	Order 2	1	.	.	.	.	.	.	.	.	1	100·0	.	.
	Orders 3, 4 and 5	2	.	.	.	.	.	.	.	.	.	.	2	100·0
	All breeding colonies	10	.	.	1	10·0	3	30·0	1	10·0	3	30·0	2	20·0
	Total all colonies	14	.	.	1	7·2	3	21·4	2	14·3	4	28·6	4	28·6
1909	Order 0	11	.	.	3	27·3	4	36·4	3	27·3	1	9·1	.	.
	Order 1	14	.	.	6	42·8	3	21·4	4	28·6	1	7·1	.	.
	Order 2	13	.	.	.	.	3	23·1	3	23·1	4	30·8	3	23·1
	Orders 3, 4 and 5	2	.	.	.	.	.	.	.	.	.	.	2	100·0
	All breeding colonies	29	.	.	6	20·7	6	20·7	7	24·2	5	17·2	5	17·2
	Total all colonies	40	.	.	9	22·5	10	25·0	10	25·0	6	15·0	5	12·5
1919	Order 0	26	3	11·5	8	30·8	9	34·7	5	19·2	1	3·8	.	.
	Order 1	31	1	3·2	11	35·5	12	38·7	5	16·1	2	6·5	.	.
	Order 2	25	.	.	2	8·0	6	24·0	9	36·0	6	24·0	2	8·0
	Orders 3, 4 and 5	6	.	.	.	.	1	16·7	1	16·7	1	16·7	3	50·0
	All breeding colonies	62	1	1·6	13	21·0	19	30·7	15	24·2	9	14·5	5	8·1
	Total all colonies	88	4	4·5	21	23·8	28	31·8	20	22·7	10	11·4	5	5·8
1929	Order 0	39	2	5·1	14	36·0	12	30·8	10	25·6	1	2·6	.	.
	Order 1	50	4	8·0	17	34·0	16	32·0	11	22·0	2	4·0	.	.
	Order 2	29	1	3·4	7	24·2	10	34·5	8	27·5	2	6·9	1	3·4
	Orders 3, 4 and 5	19	.	.	.	.	3	15·8	6	31·6	6	31·6	4	21·1
	All breeding colonies	98	5	5·1	24	24·5	29	29·6	25	25·5	10	10·2	5	5·1
	Total all colonies	137	7	5·1	38	27·7	41	29·9	35	25·5	11	8·0	5	3·7
1939	Order 0	61	1	1·6	21	34·4	21	34·4	13	21·3	4	6·6	1	1·6
	Order 1	98	10	10·2	36	36·7	30	30·6	16	16·3	5	5·2	1	1·0
	Order 2	76	2	2·6	19	25·0	29	38·2	19	25·0	4	5·3	3	3·9
	Orders 3, 4 and 5	34	1	2·9	2	5·9	11	32·4	9	26·5	7	20·6	4	11·8
	All breeding colonies	208	13	6·2	57	27·4	70	33·6	44	21·2	16	7·7	8	3·8
	Total all colonies	269	14	5·2	78	29·0	91	33·9	57	21·2	20	7·4	9	3·4

From a consideration of table and figures we may come to the following conclusions:

(*a*) There has been a general tendency, as time goes on and as population gets higher, to seek lower cliffs, i.e. breeding-cliff selection is somewhat

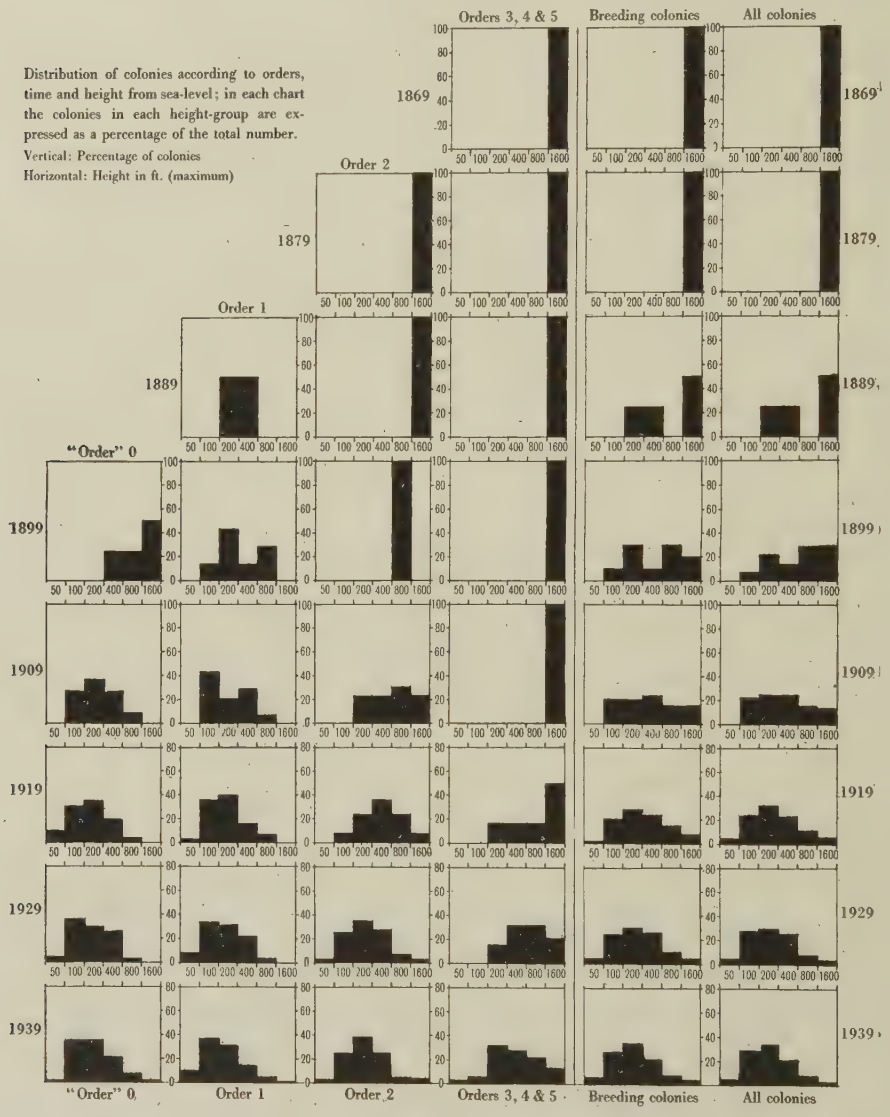


Fig. 16.

plastic. There are special exceptions to this tendency; thus in 1929 birds were prospecting cliffs (i.e. in Order 0) mostly between 50 and 100 ft., while in 1939 they were mainly prospecting cliffs between 50 and 200 ft.; and in 1909 the smallest colonies (i.e. in Order 1) were established mainly on cliffs under

100 ft.; in 1919 under 200 ft., and in 1929 under 100 ft. again. (*b*) The lower limit of tolerance seems to be about 50 ft. from sea-level. Though birds will exceptionally nest under 50 ft. their selection of such sites is rather irregular, and there is no evidence that any tendency to such selection has become truly progressive during the period under review (the tendency to select sites between 50 and 100 ft. high *has* become progressive). (*c*) Generally speaking, the higher the cliff the larger the colony, and the earlier the colonization. (*d*) On the other hand, colonies of the larger orders (2 to 5) have also shown, when grouped together, a general tendency to become established on lower cliffs. In 1939 the greatest percentage of colonies of Orders 3, 4 and 5 were dis-

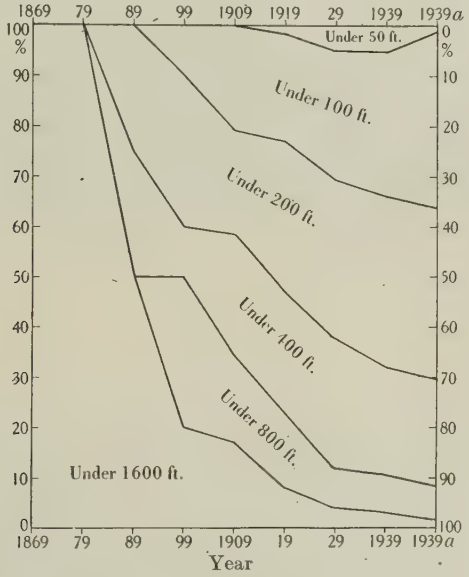


Fig. 17. Percentages of breeding colonies according to height-groups from 1869–1939. The figures for 1939*a* refer not to the breeding colonies in 1939 but to the colonies in Order 0 in that year; they thus give an indication of the continuation of the general trend.

tributed between 100 and 400 ft.; Order 2 between 100 and 200 ft., Order 1 between 50 and 100 ft.; and Order 0 between 50 and 200 ft. In 1919 the corresponding heights were Orders 3, 4 and 5, 800–1000 ft.; Order 2, 200–400 ft.; Order 1, 100–200 ft.; Order 0, 100–200 ft. (*e*) Since 1919, the majority of all the colonies, and of all the breeding colonies, has been distributed under 200 ft., and the greatest percentage between 100 and 200 ft. There is every indication that, in future years, an even greater proportion of the colonies will become established between 50 and 200 ft. from sea-level. (*f*) To sum up; in Britain the fulmar first colonized the oceanic headlands, islands and large cliffs, but it is now progressively seeking the less oceanic coasts and smaller cliffs above 50 ft.

(2) *Inland.* In the previous subsection we have recorded that the fulmar has been found breeding inland, up to one mile in Bear Island and up to 20 miles in Spitsbergen. In Britain fulmars breed inland in the following places (present status indicated by orders):

(*a*) *Bamburgh, Cheviot*; basalt crag ¼ mile from sea. Birds may have first bred here in 1928, and certainly bred in 1934 (Order 1).

(*b*) *Sandstone ravine about a mile from the sea (loc. not specified further), Morayshire.* Birds found breeding in 1928 (Order 1).

(*c*) *Rosemarkie, East Ross.* Precipitous glen ¾ miles inland. First found breeding 1938 (Order 1).

(*d*) *Eynhallow, Orkney.* First proved to breed in 1924, the fulmar was, by 1932, breeding in a ditch in the middle of the island, in the ruins of the monks' barns, and in dry stone walls. By 1935 it was even breeding on grassy ground in the middle of the island (Order 2).

(*e*) *Sanday, Orkney.* Fulmars first bred in Northwall in 1926, and by about 1933 were breeding in the mouths of rabbit burrows up to 100 yards from the sea (Order 3).

(*f*) *North Ronaldshay, Orkney.* Possibly the fulmar first bred here in 1919. Certainly by 1934 birds were nesting in ruins 300 yd. from the sea, and by 1937 were nesting on the walls and roofs of buildings in daily use (Order 3).

(*g*) *Sumburgh Head, Shetland.* Fulmars first bred here in 1907. By 1918 they were coming inland to display on the garden walls round Sumburgh House, on the broch at Jarlshof, and on the jetty at Grutness. Since 1921 they have nested on the links, some hundreds of yards inland (Order 3).

(*h*) *Mousa, Shetland.* Breeding here in 1913 (or before), by 1934 a few pairs were nesting on flat ground, about 150 yd. from the sea (Order 2).

(*i*) *Cliffs with beaches below.* At Marshall Meadows and Peasedean in Berwickshire, at Tantallon Castle in East Lothian, and at Rosemarkie village in East Ross (a colony distinct from that in (*c*)), fulmars are now breeding on cliffs separated from the sea by a substantial beach; and similar cliffs are being prospected at Sheringham in East Norfolk (1940), at St Bee's Head in Cumberland (1938) and at Caiplie in Fife (1934).

Conclusions. From a study of these examples we can conclude that three small isolated colonies (*a*, *b*, *c*) have been established some distance inland, and that five large colonies in Orkney and Shetland (*d*-*h*), originally established on coastal (but not necessarily high) cliffs have spread inland. We can also conclude that inland breeding is an interesting, but at the present time not a very important, trend of the spreading fulmar.

Non-breeding occurrences inland. We have already noted (p. 244) that in Bünsow Land, Spitsbergen, fulmars regularly fly across the mainland from Sassen Bay to Stor Fjord. In Britain we have only one record of such inland flight; in Northumberland a fulmar has been seen flying 5 miles from the sea (**210**). After storms, etc., fulmars have been found many miles inland. One found in Ontario was 40 miles west of Ottawa, and 400 miles from salt water (**297**). In central Europe they have been blown inland to Saxony (**671**), and Slovenia (**500**) as well as other places.

(3) *Nest site.* The typical site for a fulmar to nest is on a steep slope (60° and over), rather than on a true cliff. In places (i.e. most of the British and Iceland stations), where such slopes are covered with vegetation, the fulmars

Photo J. Fisher, 1937

Photo 8. Fair Isle, Shetland. A fulmar flying along the north-east cliffs, in the typical manner of this species while prospecting a new breeding-station. Fulmars may hug cliffs in this way, in the breeding-season, for many years before they finally settle and produce eggs.

Photo J. Fisher, 1939

Photo 9. Fulmars breeding on a buttress of Conachair, the great cliff of Hirta, St Kilda; typical nest-sites among vegetation on a slightly sloping cliff-top.

Face page 248

nest freely among the plants. Often these steep grassy slopes lie above the cliffs, and it is easy to see the difference in the fulmar's nest site selection from that of the other cliff-nesting birds. In Spitsbergen the fulmars occupy the zone below the glaucous gull and above guillemots; in Shetland the zone below the herring, greater and lesser black-backed gulls, and above gannets, kittiwakes and guillemots. The material used for the nest is scanty (when present at all) and may contain grass, stems of sea-pink, thrift, soil, sand, flat flaky stones, or pebbles.

However, many other sites have been recorded. In Shetland, fulmars have been found nesting on the tops of sand-dunes, in Orkney on a low sandy bank 4–10 ft. above the sea. In Iceland they may nest on screes. The variety of such exceptional sites show that the fulmar is considerably plastic in its habitat selection, and it comes into contact and often competition with many other species of animals. These animals are:

(*a*) Man. On North Ronaldshay fulmars were nesting on ruined crofts in 1934, and on inhabited dwellings in 1937. Here the highest nearby cliff is only 30 ft. high. All over Orkney and Shetland fulmars use crofts, ruins, brochs and walls for display places.

(*b*) Rabbit (*Oryctolagus cuniculus*). On Sanday, Orkney, fulmars nest in the entrance of rabbit burrows on low ground. On Fair Isle, Shetland, they do the same at the tops of cliffs. In Yorkshire a fulmar has been observed to pick up a young rabbit 8 in. long, and fly with it.

(*c*) Cormorant (*Phalacrocorax carbo*). On Nolsø, Faeroe, fulmars arrived in about 1892. At this time there was a large colony of cormorants. By 1895 the fulmars were increasing, and there were only 25 pairs of cormorants. In 1900 there were only 4 pairs, and a few years later there was none.

(*d*) Shag (*Phalacrocorax aristotelis*). On Noss, Shetland, fulmars were encroaching in 1938 and 1939 into sheltered, flat corners of rock on which shags were nesting. The sites of the two birds, which were seen nesting side by side, were qualitatively indistinguishable.

(*e*) Gannet (*Sula bassana*). On Myggenaes, Faeroe, where fulmars arrived in about 1860, they began to oust gannets from their sites. To-day (1939) they are, however, no longer competitors. On Sula Sgeir fulmars have increased, while gannets have decreased (the latter decrease being probably due to human agency). Fulmars now (1939) occupy much of the area of flat, stony ground deserted by the gannets.

(*f*) Arctic tern (*Sterna paradisaea*). On level ground in Sanday, Orkney, fulmars nest among Arctic terns.

(*g*) Herring gull (*Larus argentatus*). Many of the observers who returned inquiry forms recorded that fulmars were driving out herring gulls from their sites. Normal herring gull sites are, indeed, closer than those of other birds to normal fulmar sites. On North Rona fulmars have been observed incubating herring gull eggs on typical herring gull sites. From Yorkshire, Caithness, Lewis, Orkney and Shetland come many accounts of physical attacks by fulmars on herring gulls, ending almost inevitably in victory for the fulmar. The lesser black-backed gull (*Larus fuscus graellsii*) tends to nest on less steep slopes than the herring gull. Although, for this reason, it may less often come in contact with the fulmar, it may very well be the subject of remarks (similar to the above) that informants have sent in about 'gulls'.

(*h*) Kittiwake (*Rissa tridactyla*). In Iceland the fulmar, at times, uses ledges suitable for the kittiwake. In Sutherland, and on Foula, Shetland, it has been observed gradually to usurp such ledges, though on Fair Isle, Shetland, the kittiwakes have apparently held their own and even increased.

(*i*) Razorbill (*Alca torda*). As long ago as 1897, fulmars were using razorbill ledges on Hermaness, Shetland. This habit is particularly noticeable on Dún, St Kilda, where fulmars and razorbills nest among loose and broken rocks, and in crevices, in close association.

(*j*) Guillemot (*Uria aalge*). The typical flat nesting ledges of the guillemot have attracted fulmars, as has been noticed from Faeroe (particularly Store Dimon) and from St Kilda. In every case the impression has been that the fulmars were 'pushing out' the guillemots.

(*k*) Puffin (*Fratercula arctica grabae*). On Mingulay, Outer Hebrides, fulmars were reported to be 'driving away the puffins' in 1934. At Sumburgh Head, Shetland, the fulmar now nests in burrows among the puffin colony—sometimes several feet in under large boulders of loose stone.

(**25, 28, 46, 61, 150, 178, 223, 228, 243, 245, 337, 411, 424, 435, 440, 461, 479, 512, 524, 555, 558, 657, 784, 790, 819, 848, 858, 942, 955, 963, 964, 967.**)

(*c*) *Colony establishment, social effect of numbers, and the breeding season*

The study of the colonization of any social sea bird, such as the fulmar, cannot be relinquished without proper examination in the light of the very interesting suggestions of Fraser Darling (**219**). Though, with reference to the spread of the fulmar, he adhered strongly to the 'St Kilda theory', a passage from his book is well worth quoting (p. 93): 'The population of fulmars on St Kilda may have been kept absolutely stationary by the islanders' annual harvest, but it is more probable that along with occasional small decreases there would be slight increases as well. I suggest that such small increases, which may have resulted in some budding from the main stock, were never sufficient to allow of a large enough *initial* stock of adults forming a breeding colony elsewhere. One or two pairs are not enough to found a new colony. Once the birds were free they were but little molested at the new stations and they have continued to increase. The threshold of numbers in the completion of the breeding cycle in this species makes for an all-or-none action in its diffusion.'

We have shown (we think conclusively) that the beginning of the spread of the fulmar did not coincide with any generalized diminution of fulmar eating on St Kilda. As a matter of fact Table 7 (p. 237) shows that between 1874 and 1889 (the critical years) the human population, and highly probably also the number of fulmars taken, was on the increase. Nevertheless the fulmars which colonized other parts of Britain from 1878 onwards must have come from somewhere—and may indeed have come from St Kilda. And Darling's suggestion of the necessity for the presence of a threshold number of birds at a colony before breeding can take place, must still be considered. Darling's work, applied mostly to the herring gull, suggests that the actual numbers of the birds in a colony have an effect on the breeding efficiency of the colony as a whole. He holds that a colony of large numbers has an advantage over one of small numbers in that the stimulus—through mutual display and other social activities—which brings the birds into breeding condition at the most

suitable time, is greater in the large colony, and that furthermore, in a large colony there is, through this, more likelihood of the birds reaching the same stage of their cycle at the same time, which has advantages in the protection of the young (which are thus all at the same stage too) against predators.

In the fulmar Darling suggests that social stimulus is of such importance in the breeding cycle, that without an adequate amount of it the birds cannot prolong this cycle even to the egg-laying stage. Indeed, the fulmar has a very complicated and stereotyped display. (It has been well described in **82**, **263**, **571**, **621**, **677**, **722** and **796**.) The habit of 'visiting', in which birds visit each other's nest sites and go through a bowing display, must be particularly important as a social stimulus. Our inquiry has produced evidence which throws some light on the social effect of numbers on the colonizing fulmar.

This evidence is of three sorts, and concerns: (1) The number of years during which a colony is prospected before breeding first takes place; i.e. the number of years during which the colony is in Order 0. (2) The number of pairs that produce eggs or young in the smaller colonies, as compared with the larger ones. (3) The dates of arrival and departure and the dates of egg laying, egg hatching and young flying, i.e. the breeding season in the generally accepted sense.

Let us examine this evidence in the light of the information available.

(1) The early history of by no means all the colonies is at all complete. Let us, however, consider the 75 breeding colonies whose early observations (see p. 206) obey one or more of the following rules: (*a*) To have been made in at least four of the first ten years of the colony's history. (*b*) If the colony has not been a breeding colony for as much as ten years, then to have been made in at least half the years it has been a breeding colony (excluding 1939, if 1939 is the sole year in which the colony was observed). (*c*) If the colony has been observed in Order 0 in one year, and in a breeding order in the next.

For each of these colonies we have recorded the number of years between its first record as a colony and its first record as a breeding colony (i.e. the number of years spent in Order 0). We can construct a table showing the results:

Table 10

(No records of 17–20 years or 22 or over.)

No. of years in Order 0:	0	1	2	3	4	5	6	7	8	9
No. of colonies:	6	14	9	9	10	11	3	0	4	1
No. of years in Order 0:	10	11	12	13	14	15	16	...	21	
No. of colonies:	2	0	1	0	1	1	2	...	1	

This gives us 75 breeding colonies with a mean number of years in Order 0 of approximately 4·4. We can conclude that fulmars may very occasionally (in less than one case out of ten) breed in the year in which they first prospect a new rock. They have been found breeding in the first year after the first prospecting, more often than in any other year, but this does not fairly

represent the general tendency, which is to breed in the fourth or fifth year, as the mean figure suggests and as a clear peak in the figures also suggests. The prospecting period has been known to be over ten years in six cases: Cadboll, East Ross (12 years), Bass Rock, East Lothian (14), Redcliffe, north-east Yorkshire (15), Farne Islands, Cheviot (16), Tiumpan Head, Lewis (16) and the Knab, Lerwick, Shetland (21). Clett Head, Whalsay, Shetland (it might be added) had birds prospecting for at least 15 years before they finally bred; but the colony does not obey the rules set out above and has not been included in the table. In 1939 birds were prospecting at 61 stations, and breeding at 208.

(2) *Number of pairs present at a colony, compared with the number of eggs or young produced.* There may be as many as 50 pairs present at a colony from April to June without breeding taking place (example Handa, Sutherland, 1902). Statistics of the actual number at Order 0 colonies are available; but all that need be said here is that the presence of a dozen or more pairs, prospecting sites, displaying, or apparently incubating, should on no account be taken as an indication of breeding. From 63 observations on breeding colonies details are available of the actual numbers of pairs present, and the number of eggs laid or young produced in the season. A plotting of the number of pairs against the number of eggs produced a poor figure, obscured by much randomness and small-number effect; on the other hand a 'lumping' of the information gave us the following facts. (*a*) 48 observations of colonies in Order 1 showed that 532 pairs produced 126 eggs (or in the absence of eggs observed, young), i.e. 23·6 % bred successfully. (*b*) 12 observations of colonies in Order 2 showed that 734 pairs produced 308 eggs or young, i.e. 41·8 % bred successfully. (*c*) Such observations of large colonies as are of use in this respect show that when over 100 young are produced, the number of pairs present is not greatly in excess of their number. Certainly on St Kilda, North Rona, Sula Sgeir and Noss the birds have a breeding-success which may well be over 75 %.

Hence we may conclude that Order 1 colonies have poor breeding-success, Order 2 colonies good, and large colonies excellent. Though these figures might be regarded as side-products of the inquiry and the literature-search, they give one of the first statistical indications of the social effect described by Fraser Darling.

(3) *Dates of arrival, breeding and departure.* All reliable dates bearing on arrival, breeding and departure, both at non-breeding and breeding colonies, were collected and summarized as in Table 11, from which Fig. 18 has been constructed. For this purpose the previous definition of an observation has been used, viz. a visit to a station in a particular year. Thus arrival dates were charted as the earliest date upon which fulmars were seen at a colony in any one year.

In plotting arrivals, only the first four months in which arrivals have been noted were considered; although laggards may often come in months later

Photo J. Fisher, 1938

Photo 10. Noss, Shetland, an early fulmar station. Birds first bred in 1898. In this photo one of a pair incubates while the other greets a 'visitor'. The habit of 'visiting' appears to be an important part of breeding-season display, though its function is somewhat obscure.

Photo J. Fisher, 1938

Photo 11. Mousa, Shetland. A fulmar incubating on a rocky ledge on the low eastern cliff of this island. Fulmars often select nesting-sites suitable for guillemots, razorbills, shags and other cliff-breeders, and so compete with these species.

Face page 252

than the last of these. Breeding dates were summarized on a weekly basis, those for fledging, i.e. young flying, being lumped with departure dates, since

Table 11. *Comparison of the annual cycle of the fulmar when present at stations in the non-breeding state (Order 0) and when present and breeding at stations in small numbers (Order 1) and in larger numbers (Orders 2–5). Figures are based on percentages of the total number of observations.**

	Order 0	Order 1	Orders 2–5
Arrivals:			
First date	6 January	5 December	5 November
November	—	—	24·2 %
December	—	25·0 %	34·5 %
January	15·6 %	37·5 %	10·3 %
February	13·3 %	16·7 %	3·4 %
March	26·7 %	20·8 %	—
April	44·4 %	—	—
Last date	—	5 May	30 March
No. of observations	45	24	29
Egg-laying:			
First date:	—	20 May	12 May
Begins	—	(? 23 April)	(? 1, 2, 3 May)
Week 17, 23 April	—	(Not accepted)	—
Week 18, 30 April	—	—	(Not accepted)
Week 19, 7 May	—	—	17·6 %
Week 20, 14 May	—	5·6 %	35·3 %
Week 21, 21 May	—	33·3 %	41·3 %
Week 22, 28 May	—	27·8 %	5·9 %
Week 23, 4 June	—	33·3 %	—
Last date	—	9 June	30 May
No. of observations	—	18	17
Egg-hatching:			
First date:	—	25 June	28 June
Begins	—	(? 6 June)	—
Week 23, 4 June	—	(Not accepted)	—
Week 26, 25 June	—	11·1 %	7·1 %
Week 27, 2 July	—	11·1 %	7·1 %
Week 28, 9 July	—	55·6 %	64·4 %
Week 29, 16 July	—	22·2 %	21·4 %
Last date	—	16 July	18 July
No. of observations	—	9	14
Fledgings† and departures:			
First date	—	11 July when eggs or young destroyed	2 July when eggs destroyed
First date fledging	—	23 August	23 August
July	42·1 %	None, unless eggs or young destroyed	None, unless eggs or young destroyed
August	36·8 %	38·1 %	40 %
September	21·1 %	61·9 %	60 %
Begins			
Week 34, 20 August	—	19·1 %	30 %
Week 35, 27 August	—	23·8 %	20 %
Week 36, 3 September	—	42·8 %	40 %
Week 37, 10 September	—	14·3 %	10 %
Last date	7 September	12 September	13 September
No. of observations	19	21	20

* See p. 206. † I.e. young leaving the nest.

the two are almost coincident. Departure dates for the non-breeding colonies were, however, plotted on a monthly basis (July to September). In non-breeding colonies it is impossible to distinguish between the last arrival-dates

and the first departure-dates, since birds may come and go even in May and June at these stations. We can reach the following conclusions:

(*a*) At non-breeding colonies fulmars arrive on 6 January at the earliest (Chickens Rock, Calf of Man, 1934) but mostly arrive in April. Most leave in July, a large number in August, and a few in September, the latest dates being 5 September (Rhu Stoer, west Sutherland 1937) and 7 September (Stacka, and Calf of Man, 1933).

(*b*) At small colonies (Order 1) birds mostly arrive in January, the earliest arrival being 5 December and the latest 5 May. Eggs are mostly laid in weeks 21–23 (21 May to 10 June), the earliest reliable record being 20 May and the latest 9 June (20 days after 20 May). Eggs mostly hatch in week 28 (9–15 July), the earliest reliable record being 25 June and the latest 16 July

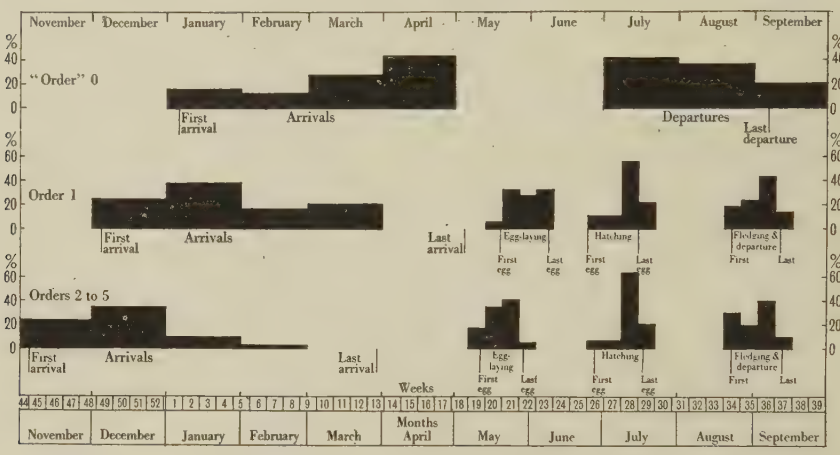


Fig. 18. Arrival, breeding and departure dates of birds at non-breeding colonies, small breeding colonies (Order 1) and larger breeding colonies (Orders 2–5). The vertical axis is used for percentages of the total number of observations that give specific dates.

(21 days after 25 June). Young fly, and the birds depart, mainly in week 36 (3–9 September); when eggs or young are destroyed birds may depart as early as 11 July; the earliest fledging (young flying) date is 23 August, and the latest 12 September (20 days after 23 August).

(*c*) At large colonies (Orders 2–5) birds mostly arrived in December, the earliest arrival being 5 November and the latest 30 March. Eggs are mostly laid in weeks 20 and 21 (14–27 May), the earliest reliable record being 12 May[1] and the latest 30 May (18 days after 20 May). Eggs mostly hatch in week 28 (9–15 July), the earliest record being 28 June and the latest 18 July (20 days after 28 June). Young fly, and the birds depart, mainly in week 36 (3–9

[1] Though 2 May has been recorded by a lighthouse-keeper from Sumburgh, Shetland, in 1918, and Martin Martin, Gent (**486**, pp. 30–1) writes—about the bird on St Kilda—'it lays its Egg commonly the First, Second, or Third Day of *May*'; but Martin recorded hatching in the middle of June, and flying on 20 July, both of which are absurd.

September); when eggs or young are destroyed birds may depart as early as 2 July; the earliest fledging date is 23 August, and the latest 13 September (21 days after 23 August).

(*d*) Not only, then, is the date of arrival a month or more earlier when the birds are breeding than when they are merely prospecting a station, but the date of arrival is a further month earlier at a large (Order 2 or over) colony than at a small one (Order 1). Birds at non-breeding colonies tend to depart as early as July, a month in which breeding-colony birds only depart if their cycle has been interfered with by the destruction of eggs or young (there is no evidence that the fulmar lays again if its egg is lost).

Egg laying tends to be about a week earlier, and to take place over a slightly shorter period in the larger, as opposed to the smaller colonies. Egg hatching takes place at about the same time in large and small colonies, and occupies about the same period. Fledging and departure take place at the same time, and occupy the same period, in both large and small colonies.

The interval between the peak laying time and the peak hatching time is seven weeks, and between the latter and the peak fledging time eight weeks. This corresponds quite well with what is known of the fulmar's incubation and fledging periods, which are as follows:

Incubation period

	Days
Baxter & Rintoul (**39**), North Unst	*c.* 56
Rintoul & Baxter (**612**), North Unst	42
Mackenzie (**465**), St Kilda	*c.* 42
Robinson (**632**, **633**, **634**), Orkney	40 or 41
Robinson (**635**, **636**), Bass Rock	44
Richter (**608**), Morayshire	57, 55–57
Saemundsson (**655**), Iceland	42–49

Of these, the first may not be very accurate. Without using the general figures given by Bent (**67**), 50–60 days, and Thienemann (**732**), 56–60 days, and discarding MacGillivray's, 1 month (**462**), we can conclude that the normal incubation period is 47 or 48 days, occasionally a week less or a week more, i.e. generally from 6 to 8 weeks.

Fledging period

	Days
Rintoul & Baxter[1] (**612**), North Unst	48
Robinson (**632**, **633**, **634**), Orkney	57
Levett (**427**), Northumberland	56
Levett (**429**), Northumberland	46–53

These give us a mean figure of about 53 days; and a normal fledging period of from a little under 7 to a little over 8 weeks.

In general, the effect of numbers on the fulmar's breeding cycle is parallel to the effect of numbers on the herring-gull's cycle described by Fraser

[1] Jourdain, who in 1930 (**394**) pointed out that we had only scanty data (from British sources) on the fulmar's incubation period, and none on its fledging period, had overlooked this note, published in 1913.

Darling (**219**). The fulmar is a social bird, and its breeding efficiency is, we have shown, partly a function of the intensity of its sociality. Moreover, the facts concerning the lag between prospecting and breeding, and the inefficiency of new, small breeding-colonies compared with large, point to the further conclusion that the old birds stick to one colony, while a proportion of their young become pioneers. The breeding efficiency of a fulmar colony may also depend on the age of its members.

(*d*) *Enemies of the fulmar*

In the East Atlantic there is little evidence that fulmars are preyed upon by any animals save man. Even in Spitsbergen there is no proof that the arctic fox ever tackles the fulmar, though it can often reach its nest site. In Britain it has only been once suggested—Skye (Floddigarry)—that peregrines drive fulmars away from their sites; certainly fulmars nest within a few yards, or even feet, of peregrines on St Kilda, Noss, Handa, Foula and Hermaness. Gulls, particularly the great blackback (*Larus marinus*) will take the eggs of fulmars if they are left unprotected; but as far as can be seen this only happens if man appears on the scene and drives the bird off its egg. Neither the great blackback nor the great skua (*Stercorarius s. skua*) can drive the fulmar off its food. Rats can kill a captive fulmar. In the Pacific fulmars are preyed on by the Northern bald eagle (*Haliaëtus leucocephalus alascanus*); this eagle lives mainly on birds in the Aleutian Islands (59 % of individuals in prey 1 year, 86 % another in 28 nests in all), and fulmars are eaten more often than any other species of bird (6·7 % of total prey one year, 22·6 % another).

Fulmars are among the few birds upon which barnacles have been found. In San Francisco Bay, California, 2 female *F. g. rodgersii* were shot on 7 August 1938 with small clusters of young peduncled barnacles (*Lepas hillii*) attached to the outer barbs of their belly feathers. The particular individuals must have been in the water most of their time for the barnacles to have reached their state of development. This throws a new light on the habits of (probably) non-breeding fulmars.

(**23**, **515**, **555**, **848**, **856**, **963**.)

(*e*) *Food relations*

Tempting as it is to try to correlate the spread of the fulmar with change in its food supply, we feel strongly that it would be madness to make any extravagant claims, in view of our present inadequate knowledge of recent changes in the distribution of marine plankton. The fulmar is known to eat the following foods:

Oily offal of all kinds, chiefly on water. **Mammals.** Bear, walrus, seal and whale carcases, whale dung, pork bait, floating butter, and, in captivity, hog's lard. **Birds.** Feather traces recorded in stomach, and carcases of redwing, eider, gulls sp. and puffin noted as eaten. **Fish.** Small live fish are never an important part of diet—only 6 % in Greenland; much the same in Spitsbergen. Slightly more important in winter range, e.g. on Newfoundland Banks, and (*F. g. rodgersii*) off San Diego Bay, California. Young herring (*Clupea harengus*) and

sand-eel (*Ammodytes* sp.) recorded. Carcases of fish, e.g. of herring and cod, and fishermen's bait and offal readily eaten. Fishermen's minnow bait taken by stormbound bird inland 400 miles from sea. **Mollusca.** *Cephalopoda* appear to be almost universal in diet; most evidence comes from the presence of beaks and lenses in stomach contents. Squids, e.g. *Sepia* (also found in *rodgersii*) and *Loligo* are commonly taken, particularly in summer range (in 100 % Greenland and Pribilov (*rodgersii*) stomachs). *Gastropoda.* Pelagic forms common in diet; Pteropods often recorded, e.g. *Limacina arctica* and *Clio.* **Crustacea.** Planktonic Crustacea form highly important and often preponderant part of diet; responsible for redness of fulmar oil. Red colour due to presence of *astacin* which, in fulmars as in whales, may be used to produce vitamin A. Fulmar oil is as rich in vitamin A as is cod-liver oil, and also contains vitamin D. It is very much like sperm oil in composition. Crustacea known to have been taken are *Hymenodora glacialis* (Jan Mayen), *Thysanoessa inermis* (important in the inner fjord zone of Spitsbergen), *Pseudalibrotus littoralis* (Spitsbergen), *Euthemisto libellula* (Greenland and Spitsbergen), *Mysis oculata* (Spitsbergen), Copepods, including *Calanus* (Faeroe), and *Hyperoche kroyeri* (an Amphipod parasitic on the Coelenterate *Cyanea*, probably taken with its host). **Annelida.** Pelagic marine Annelid worms, particularly Nereids, have been found in the stomachs of fulmars in Greenland and in the Canadian Arctic. **Nemathelminthes.** Chaetopods. *Sagitta elegans arctica* has been recorded (Spitsbergen). **Nematoda.** Found in stomachs in their own right, also probably by having been eaten together with host, e.g. cod's liver. **Coelenterata** appear to be a very important part of fulmar diet: indeed Procellariiform birds alone appear to feed on planktonic Coelenterates to any extent. *Ctenophora.* Beröe (Greenland) is recorded. *Scyphozoa.* Probably more common in diet than is generally imagined, owing to the difficulty of identification in stomach contents. *Aurelia aurita* (Britain), *Cyanea capillata* (Spitsbergen) and large jellyfish (California and Bering Sea) recorded (the latter in *rodgersii*). **Vegetable matter.** Vegetable debris is often present in the stomach in small quantities. The following have been noted: algae, including seaweed-bladders, *Zostera*, *Cochlearia*, *Carex* and *Rumex*; also seeds and wood-fibre. Grit and stones have also been recorded in stomachs.

(21, 24, 26, 65, 74, 147, 194, 195, 203, 212, 248, 255, 297, 312, 334, 353, 354, 355, 444, 479, 480, 499, 513, 514, 534, 539, 586, 608, 641, 648, 657, 706, 716, 795, 796, 848, 873, 874, 939.)

To sum up, the fulmar is primarily a plankton feeder, but it eats in addition any other oily matter it can get. Some of the kinds of plankton which it eats, like Coelenterates, are, we suspect, not eaten by other sea-birds save petrels, or readily by fish.

It has been suggested that the first spread of the fulmar—to the Shetlands—may have been correlated with changes in plankton distribution, themselves linked with the change in the herring fishery from sail to steam, and from grounds close to land to grounds further out to sea. In this respect the following points are worthy of mention. The herring moved further to sea owing probably to changing ocean currents which carried the richer plankton food further away from Shetland than was formerly the case. (*Informant* (**860**), who points out that this is a speculation.) The Faeroes have only a minute herring industry, and were colonized by the fulmar between 1816 and 1839. Norway has a flourishing herring industry, and was only colonized in a small way in 1924. We can conclude that changes in the herring fishing grounds in Shetland were probably due to the fact that the herrings *followed*

the plankton, rather than that the inshore waters got 'fished out'. It cannot be supposed that the fulmar colonized Shetland because of any increase of plankton due to the departure of the herrings. (Fulmars first bred on Foula in 1878 when a whale was being cut up there.) Correlations may exist between the spread of the fulmar and its food, but it will be a Herculean task to discover them. In any case, we feel that since the tightest limits of the life of some northern sea birds seem to be imposed on them by their nest habitat selection, and by the amount of such habitat available for them to select, it will be more useful, for the moment, to concentrate on matters of this sort.

6. The future of the fulmar in Britain

The increase of the fulmar in Britain will certainly continue. There is no reason to suppose that breeding can be long delayed at any of the present non-breeding stations. In a few years some observer will find an egg or young in Cumberland,[1] on Great Orme's Head, on Holyhead, in Pembrokeshire, on Lundy, in Cornwall or the Scillies, and possibly in Norfolk and France. In fact we can suggest little to stop the fulmar breeding eventually on every suitable cliff above 50 ft. in Britain, and on some below this height. But there are signs that the geographic spread is reaching its limits. On the east coast it reached the southward limit of high cliffs in 1922, though the recent (1940) prospecting of east Norfolk leads us to believe that it may shortly breed on the fairly low cliffs here. On the west it has more cliffs to conquer if it rounds the corner of Cornwall. We shall soon know whether the 60° F. July isotherm is an important barrier; the test will be whether or not the fulmar arrives on the cliffs of the Isle of Wight, or establishes itself on those of north-west France.

The increase shows little sign of flagging, though the curve in Fig. 14 is beginning to show a very slight tendency towards flattening. There is plenty of room for increase in the number of breeding birds at every one of the existing colonies, and when the normal nest sites are exhausted there is no reason to suppose that the bird may not turn its attention to herring gull, guillemot or razorbill sites.

This paper has attempted to give the picture of the fulmar in Britain up to 1939. We shall be glad if it stimulates others to take an interest in the distribution of this magnificent bird, and we hope that they will find it a yard-stick by which to measure its change in the future. In particular we can suggest another inquiry at the end of the next five-year period—in 1944, or at least in 1949; and that particular attention should be paid to breeding population, in order to avoid the necessity of using the logarithmic method again.

[1] This has now (1941) come to pass.

7. SUMMARY

1. From 1934 to 1939 the British Trust for Ornithology undertook investigations into the breeding distribution of the fulmar, *Fulmarus g. glacialis* (L.) in the British Isles. 172 individuals took part. This paper gives the results of these investigations, and incorporates previous published accounts.

2. Observations on the fulmar's distribution were most intensive in the periods 1880–9, 1910–14, and 1930–9.

3. Observations in space were most intensive in England, Wales, the west Lowlands, and the east of Ireland, and least intensive in the north Highlands, Orkney, Shetland and the south-west of Ireland.

4. Observers' notes of the population of each colony were recorded as *Breeding not proved* (Order 0), *Breeding Order* 1 (where under 10 eggs or young were produced), *Order* 2 (under 100), *Order* 3 (under 1000), *Order* 4 (under 10,000) and *Order* 5 (under 100,000). The *mean* population of all colonies in Order n was taken to be $4 \times 10^{n-1}$.

5. Breeding only in St Kilda before 1878, the fulmar has spread in five main directions:

(*a*) Shetland (1878), Sula Sgeir and North Rona (1887), Orkney (1900), west Sutherland (1902), Caithness (1905), Aberdeenshire (1916), Kincardine and Banff (1920), Angus and Berwickshire (1921), south-east Yorkshire (1922), Morayshire (1923), East Ross (1924), north-east Yorkshire and Durham (1927), north Northumberland (1928), East Lothian (1930), Fife (1931), east Sutherland (1939)—present but not proved to breed east Norfolk (1940).

(*b*) Outer Hebrides (1902), West Ross (1937).

(*c*) Mayo (Ireland) (1911), Donegal (1912), Kerry (1913), Clare (1924), Galway (1932), Cork (1938), now present but not proved to breed in Waterford, Pembrokeshire, Lundy (north Devon), Cornwall, the Scillies and Ushant (north-west France).

(*d*) Antrim (1921), east Donegal (1925), Wigtownshire (1932), Isle of Man and Dublin (1936), Londonderry (1939), now present but not proved to breed in Cumberland, Carnarvon and Holyhead.

(*e*) Islay (1924), middle Inner Hebrides (1929), Skye (1930), Ailsa Craig (Clyde) (1939), now present but not proved to breed on Mull of Kintyre.

6. The breeding population of St Kilda, which is held to have remained stationary throughout, is about 21,000 breeding pairs. Since 1877 the population outside St Kilda has increased from 0 to about 40,500 breeding pairs, nesting in 208 colonies in 1939. In 1939 there were also 61 other colonies at which breeding had not yet been proved.

7. The 1939 population was distributed as follows:

England and Wales	About	240	breeding pairs
Lowlands of Scotland	,,	225	,,
Highlands of Scotland	,,	4,600	,,
Outer Hebrides, Orkney and Shetland	,,	34,500	,,
excluding St Kilda, which has	,,	21,000	,,
Ireland	,,	1,100	,,

8. From 1855 until 1921 the human population of St Kilda remained steadily in the neighbourhood of 70. There is evidence that at no time in this period did it change the quality or quantity of its fulmar-killing activities. The advent of stored food to St Kilda, which coincided with the start of the fulmar's spread, had no effect on the fowling habits. A thousand fulmars were taken every year (on an average) for every 8 inhabitants. Since 1921 the drop and final extinction of the human population on St Kilda may have had an effect on the fulmar population.

9. Increases in the fulmar population of Iceland have been recorded since about 1820, and the bird arrived as a breeding species in the Faeroes between 1816 and 1839, where in recent years (before the psittacosis outbreak traced to fulmars) over 100,000 young ones were taken annually. In Norway it first bred in 1924. It has now arrived in France in the breeding season.

10. The spread of the fulmar in Britain cannot be attributed in the long run to its relation with man on St Kilda, and is due to a biological change which is not understood.

11. Even if fulmars were immortal and perpetually fertile, probably more than, and certainly at least, one in six of Britain's fulmars must have bred in every year, at the period of maximum increase (*c.* 1927). If, as has been suggested, it is normal for one in three to breed, the normal life span must have been over 12 years.

12. The fulmar is a Palearctic breeding species with outposts only in such parts of the Nearctic as have considerable Palearctic affinities.

13. The southward limit of its present breeding distribution in both Atlantic and Pacific is bounded by the 60° F. July isotherm.

14. It has a clear preference for islands (large and small) and oceanic headlands as breeding places, but will also nest some distance inland.

15. At first the fulmar bred in Britain on the highest cliffs, over 200 ft. from sea-level, and often over 400 ft. As time went on and population increased there was a noticeable trend towards breeding on cliffs under 200 ft. However, breeding on cliffs under 50 ft., though it does occur, remains exceptional.

16. At eight stations in Britain fulmars now breed from 100 yd. to about a mile from the sea.

17. The fulmar's nest site normally differs from that of any other cliff-breeding bird which shares its distribution. However, on a breeding station its sites may overlap with those of man, the rabbit, cormorant, shag, gannet, herring gull, kittiwake, arctic tern, razorbill and possibly puffin. Its competition with these animals is often successful.

18. Fewer eggs or young are produced per breeding pair in small colonies than in the larger ones.

19. At large colonies birds arrive a month earlier than at small colonies, and two months or more earlier than at non-breeding colonies. Birds at non-breeding colonies normally depart at a time when birds at breeding colonies only depart if their cycle has been interfered with by the destruction of eggs or young just hatched.

20. Egg laying is generally earlier in the larger colonies than in the small ones, and takes place over a shorter period.

21. In a colony the social stimulus of numbers is required to enable the fulmars to go through their full breeding cycle. Members of small, new colonies are probably young birds.

22. There are no predators on the Atlantic fulmar save man.

23. The fulmar feeds on plankton and any oily matter it can get. It is not known whether there is any correlation between the changes in its distribution and in its food supply.

24. It will continue to increase and spread in Britain.

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STUDIES ON THE BIOLOGY OF THE EARLY STAGES OF THE SALMON (*SALMO SALAR*)

3. GROWTH IN THE THURSO RIVER SYSTEM, CAITHNESS

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(*With* 3 *Figures in the Text*)

CONTENTS

		PAGE
1.	Introduction	273
2.	Methods and apparatus	275
3.	Seasonal changes	277
4.	Discussion	284
5.	Acknowledgements	293
6.	Summary	293
	References	294

1. Introduction

The present series of papers deals with the results of a study of the biology of the freshwater stages of salmon which was carried out between June 1935 and October 1938. During the first part of this work observations were made on the young salmon of the river Eden (in Cumberland and Westmorland) and some of its tributaries. The results obtained concerning the growth of these fish have been set out in a previous paper (Allen, 1940). In August 1937 a study was commenced of the young salmon of some tributaries of the Thurso river in northern Scotland. The present paper describes the results obtained concerning the growth of the salmon in these waters and compares the growth of the fish in the two river systems investigated.

The Thurso river, which is situated in Caithness in north-east Scotland, flows in an approximately northerly direction and enters the sea in Thurso Bay on the north coast of Scotland after a course of 62 km. The upper part of the course lies in an open valley between hills about 300 m. high, but from Dalnawillan northwards the valley widens rapidly and for the lower part of the course is very wide and shallow. The drainage area consists almost completely of barren peat moorland in the upper part, but of agricultural land from Westerdale northwards. Fig. 1 shows the course of the Thurso river and the position of the netting areas and the places referred to in the text.

During the spring and summer salmon run up the lower part of the river and into Loch More but comparatively few enter the upper part of the river

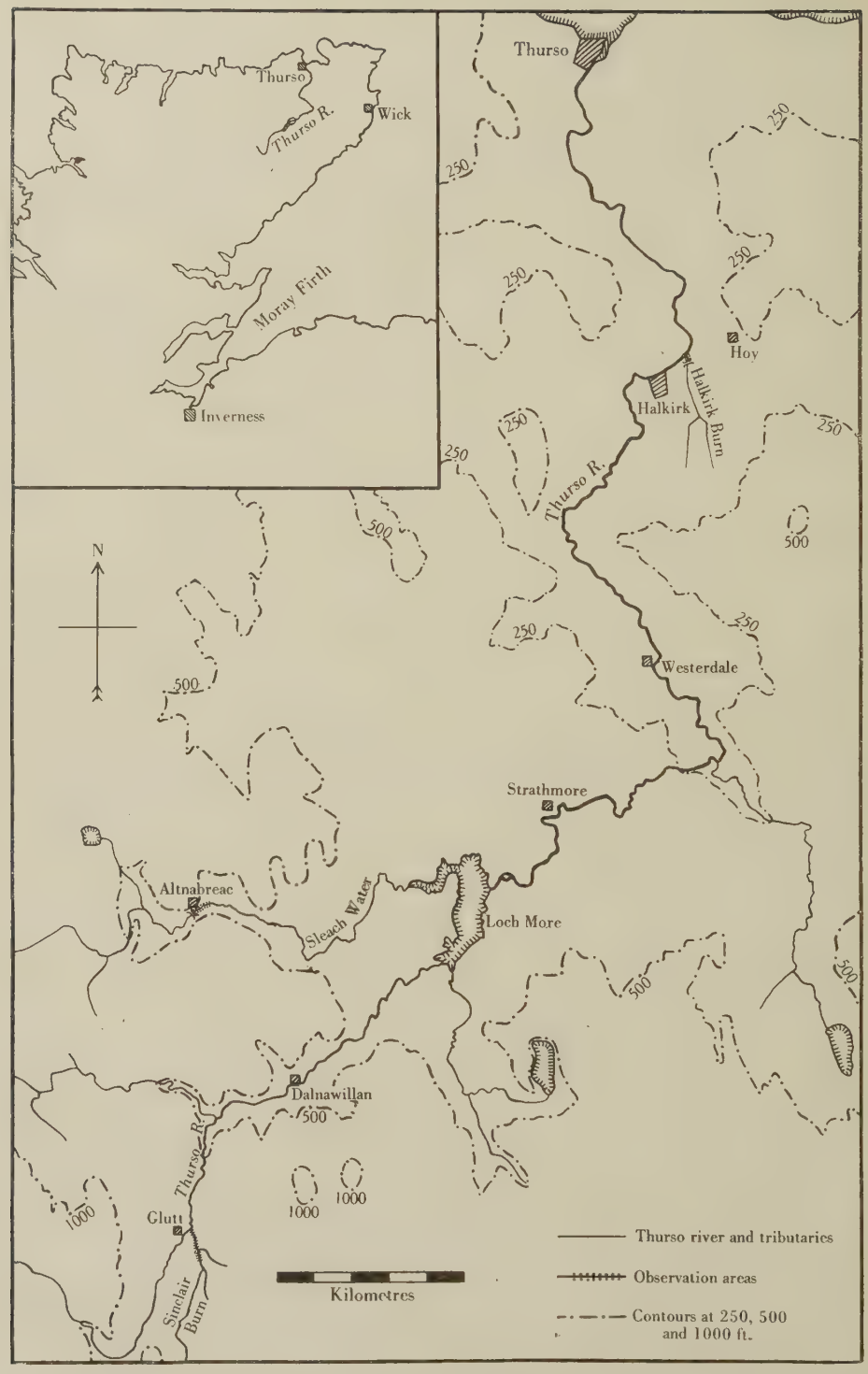

Fig. 1. The course of the Thurso river, showing the position of the observation areas and of the places mentioned in the text. [Inset, northern Scotland, showing the position of the Thurso river]

until the autumn. Prior to spawning, however, considerable numbers of fish penetrate the upper reaches of the river and salmon spawn throughout the main river as far as the falls 3·2 km. above Glutt, and in all the suitable tributaries. Salmon also spawn in the main river below Loch More, particularly in the neighbourhood of Strathmore, and in some of the lower tributaries.

Three contrasting tributaries of the Thurso river were selected in which to study the biology of the young salmon. These were as follows:

(*a*) *The Sinclair Burn.* This enters the Thurso river from the east at Glutt, about 51·5 km. from the sea. This is a rapid shallow stream, mostly about 10–20 cm. deep, with occasional pools up to 80 cm. deep. The bottom is composed in part of sand and fine gravel of about 2 cm. diameter, and in part of angular stones about 30 cm. in diameter embedded in the fine gravel. The area studied extended upwards for about 1100 m. from a point about 100 m. above the confluence.

(*b*) *The Sleach Water.* This tributary enters the Thurso river from the west at Loch More about 38 km. from the sea. The area studied extended downwards from the bridge at Altnabreac for about 870 m. and lay about 9 km. above the mouth of the stream. In this region, and between this and Loch More, the Sleach Water consists of a series of long, deep, sluggish pools, usually 60–90 cm. deep, separated by short stretches of shallow rippled water. The bottom is composed principally of sand and very fine gravel, with some gravel up to 8 cm. in diameter on the shallows. In the shallower water there are considerable beds of vegetation in which *Callitriche* sp., *Potamogeton* sp., and *Myriophyllum* sp. predominate. The drainage areas of both this stream and the Sinclair Burn are composed entirely of peat moorland.

(*c*) *The Halkirk Burn.* This enters the Thurso river from the east immediately below Halkirk about 12 km. from the sea. The area studied extended from the confluence with the main river to the bridge on the Halkirk-Hoy road. This is a shallow stream, mostly 10–20 cm. deep, with a few pools up to 50 cm. deep. It flows through agricultural land and in the area studied was overhung by willows to a considerable extent. The bottom is composed largely of angular stones 10–20 cm. in diameter.

Several analyses were made of the water of each of these streams and the mean results are given in Table 1.

Table 1. *The mean results of analysis of the water of the streams studied*

	River Eden	Sinclair Burn	Sleach Water	Halkirk Burn
*p*H	8·2	6·4	7·1	8·2
Carbonate hardness (mg./l. $CaCO_3$)	166·0	7·6	22·9	126·0
Ammonia (mg./l. NH_3)	0·05	0·0	0·03	0·0
Nitrate (mg./l. NO_3)	1·7	0·03	0·26	0·55
Silicate (mg./l. SiO_2)	3·0	2·2	1·9	2·6
Phosphate (mg./l. P_2O_5)	0·007	0·017	0·035	0·015
Oxygen absorbed (mg./l.)	2·0	12·0	10·0	5·0

2. Methods and apparatus

So far as possible the methods used in the investigations carried out on the river Eden were again used in the studies on the Thurso system. All fish examined were taken by netting, although owing to the very much smaller size of the Thurso tributaries different nets were necessary. The nets used were

however, essentially similar to those used on the Eden and consisted of a triangular trawl-shaped bag to which wings could be attached. The trawl was 2·1 m. long and had a mouth 1·2 m. high and 2·1 m. wide. It was fitted with corks and leads arranged similarly to those on the trawl described previously (Allen, 1940). Owing to the narrowness of the streams in which these nets had at times to be worked, no rigid frame could be used on the trawl, and the mouth was kept open by the corks on the head-rope and the leads on the foot-rope, and by the horizontal pull on the wings. To enable the gear to be used effectively in waters of varying width, a number of wings of different lengths were made, and in any particular water the two most suitable were attached. The lengths of the wings were 0·9, 1·8, 4·6, 9·1 and 13·7 m., and they were all 1·2 m. deep. A conical lead weight which weighed 3·6 kg. was attached to the tail of the trawl when the nets were worked downstream. The nets were made throughout of $\frac{1}{4}$ in. (0·6 cm.) knot-to-knot cotton netting, and the floor of the trawl was reinforced with heavy $\frac{1}{2}$ in. (1·3 cm.) knot-to-knot netting. The nets were mounted on 1 in. (2·5 cm.) tanned hemp ropes. In the shallow waters of the Sinclair and Halkirk Burns it was found more efficient to work the nets upstream as the current then tended to keep the trawl more widely open, but in the deeper water of the Sleach Water the nets were worked downstream satisfactorily. The method of working was essentially the same as that described for the Eden gear, except that only two men were required, one at the end of each wing. A spare wing of suitable size was used as a stop-net.

All fish caught were weighed and measured in the field, lengths being measured from the nose to the end of the shortest caudal fin ray with an accuracy of 0·1 cm., and weights being determined to the nearest 0·5 g. Smaller fish were usually weighed in batches of 6 or 10. The fish required for the examination of stomach contents were preserved in 4 % formalin and carried back to the laboratory. Here the same methods were used as in the case of the stomach-contents material from the Eden. The fish were again weighed and measured with a higher degree of accuracy than in the field, and the stomach contents were removed, examined, and finally weighed after drying for 3 days at 65° C.

Quantitative faunistic collections were made in each of the Thurso tributaries investigated on each occasion when fish were taken there. The methods used in the taking of the collection and in its subsequent treatment were those which have been fully described in a previous paper (Allen, 1940). The sample of stream bed was removed by means of a heavy iron scoop fitted with a cutting edge and a canvas bag. This sample was sieved on the spot to remove the large stones, and the finer material was preserved and carried back to the laboratory. Here it was washed to separate the animals and plant detritus from the stones and the animals were then picked out by hand, identified and counted.

3. Seasonal changes

In the river Eden certain very well-marked seasonal changes were found to take place in the growth of young salmon. The results obtained in the streams of the Thurso system have therefore been examined in order to determine how far similar effects occur there. Table 2 shows for each stream and for each year class of salmon present the mean length, weight and condition factor of each sample taken. The data regarding salmon of the 1936 year class taken in the Sleach Water between 28 April and 7 May refer to migrating smolts trapped at the mouth of this stream. With this exception all the samples were taken by netting in the portions of the streams previously described. In Fig. 2 the mean lengths are plotted against time.

It will be seen that in all three Thurso tributaries the growth curves obtained are similar in type to those obtained on the river Eden (Allen, 1940) in that the year may be divided clearly into a period of growth and a period of quiescence. The period of growth extends approximately from April to September in all these streams. The data do not show clearly whether the growth period in the Thurso system may be subdivided into an early period of rapid growth and a late period of slow growth as in the Eden. They suggest, however, that this may be the case. Comparison of the size of different year classes in the same stream at the same age shows that, as in the Eden, noticeable differences may occur between one year and the next. In the Sinclair Burn and the Sleach Water both first-year fish and second-year fish were larger at the end of the summer of 1937 than at a similar date in 1938, while in the Halkirk Burn the reverse was the case. Thus in each of the streams the difference in size between fish of the same age at the end of the summers of 1937 and 1938 is of the same sign for both first- and second-year fish. The standard deviation of the length of each of the larger samples has been calculated and it appears that in the Thurso system, as in the Eden, it is approximately 10 % of the mean length.

The condition factors in Table 2 have been calculated from the formula:

$$\text{Condition factor} = \frac{10^4 \times W}{L^3},$$

where W = weight in grams, and L = length in cm. The mean values given in the table have been determined from those fish which were carried back to the laboratory, since these were weighed with greater accuracy than those weighed in the field. As in the Eden, the summer values are markedly higher than the winter values and a rapid rise in condition factor in the spring coincides with the commencement of rapid growth. In the Thurso system, however, the condition factor appears to fall abruptly in the autumn, instead of gradually during the late summer and more rapidly during the winter.

Since the values for condition factor given in Table 2 were determined from fish preserved in formalin, an error is introduced by the shrinkage in length

Table 2. *The mean length, mean weight, condition factor (K) and number of fish measured in each collection*

Year class	Date	Sinclair Burn				Sleach Water				Halkirk Burn			
		Mean length cm.	Mean weight g.	*K*	No. of fish	Mean length cm.	Mean weight g.	*K*	No. of fish	Mean length cm.	Mean weight g.	*K*	No. of fish
1935	27–31 Aug. 1937	10·0	11·0	—	10	—	—	—	—	—	—	—	—
	19 Nov. 1937	10·3	10·9	—	4	—	—	—	—	—	—	—	—
	21 Mar. 1938	10·9	13·2	—	3	—	—	—	—	—	—	—	—
1936	27–31 Aug. 1937	8·8	7·7	123	23	11·9	19·4	144	27	9·9	11·8	135	39
	8–20 Nov. 1937	9·0	7·5	117	8	11·7	17·4	132	7	11·4	16·0	127	13
	18–21 Mar. 1938	9·0	7·2	127	4	12·3	19·9	122	7	12·6	21·5	130	6
	28 Apr.–7 May 1938	—	—	—	—	12·5	18·5	—	96	—	—	—	—
	11 May 1938	—	—	—	—	—	—	—	—	13·9	25·3	—	23
	10 June 1938	10·6	*	134	*	—	—	—	—	—	—	—	—
	8 Aug. 1938	10·7	13·4	—	8	—	—	—	—	—	—	—	—
	2 Oct. 1938	10·9	*	130	*	—	—	—	—	—	—	—	—
1937	27–31 Aug. 1937	4·7	1·1	117	104	6·2	2·6	125	66	6·4	2·9	122	54
	8–20 Nov. 1937	4·8	1·1	108	19	6·9	4·0	120	12	6·6	3·1	117	37
	18–21 Mar. 1938	5·1	1·3	107	16	6·9	3·7	115	63	7·5	4·7	124	23
	11 May 1938	—	—	—	—	—	—	—	—	8·9	7·8	—	19
	6–10 June 1938	6·2	*	132	*	9·1	*	126	*	9·4	*	134	*
	5–8 Aug. 1938	8·1	5·4	127	34	11·1	14·5	130	50	11·8	19·9	134	18
	30 Sept.–2 Oct. 1938	8·2	*	131	*	11·5	*	134	*	12·4	*	142	*
1938	6–10 June 1938	3·2	*	115	*	3·3	*	110	*	3·8	*	123	*
	5–8 Aug. 1938	4·1	0·7	120	53	5·2	1·7	130	93	6·2	2·8	139	83
	30 Sept.–2 Oct. 1938	4·5	*	121	*	5·9	*	128	*	7·3	*	134	*

* Owing to the loss of certain raw data the mean weights and number of fish measured are not available for these collections. The sizes of the samples were, however, similar to the corresponding ones of the previous summer.

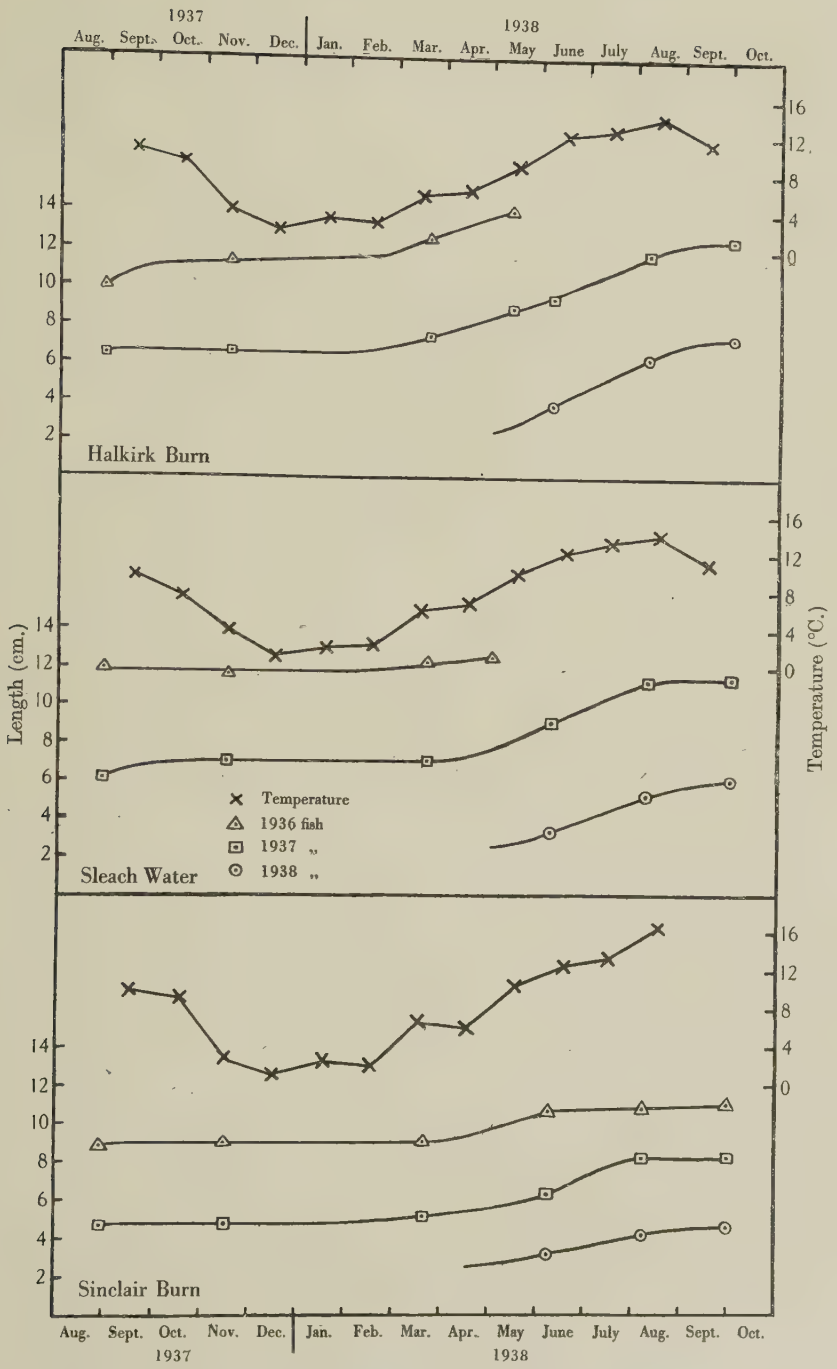

Fig. 2. The monthly mean temperature and the mean length of each year class plotted for each of the Thurso tributaries.

which occurs under these conditions. Shetter (1936) has shown that for other species of Salmonidae this shrinkage amounts to about 5·5 %. This would produce an increase in condition factor of about 19 %. Comparison of the mean condition factor of two samples of brown trout (*Salmo trutta*) taken from the Horokiwi stream in New Zealand, and measured in one case alive and in the other case after preservation for some weeks in 4 % formalin, showed an increase in the condition factor of the preserved fish of 17 %. Thus it appears probable that the condition factors given in Table 2 are about 18 % above the values which would have been obtained had the results been determined from living fish. If this is the case the condition of the young salmon is considerably poorer in the Thurso system than in the Eden system. This is confirmed by the approximate values obtained from the measurements of living fish in the Thurso system.

Table 3. *The mean quantity of food expressed as a percentage of the weight of the fish and the number of fish examined for each collection. Combined results for the three streams studied*

	Year of hatching					
	1936		1937		1938	
Date	Quantity of food	No. of fish	Quantity of food	No. of fish	Quantity of food	No. of fish
27–31 Aug. 1937	0·057	9	0·222	21	—	—
8–20 Nov. 1937	0·094	8*	0·151	15*	—	—
18–21 Mar. 1938	0·126	11	0·165	17	—	—
6–10 June 1938	—	—	0·164	29	0·353	31
5–8 Aug. 1938	—	—	0·087	23	0·173	31
30 Sept.–2 Oct. 1938	—	—	0·082	19	0·098	28

* In each of these samples 1 fish which had been feeding upon salmon eggs has been excluded on account of the relatively high dry weight of the eggs.

It was found that the quantity of food in the stomachs of the young salmon of the Eden showed definite seasonal changes which appear to be related to the seasonal changes in rate of growth. In Table 3 the corresponding data from the Thurso system are set out. The results from the three tributaries have been combined in order to obtain samples of adequate size. The figures represent the dry weight of the contents of the anterior limb of the stomach expressed as a percentage of the wet weight of the fish. Except in the case of the 1936 year class, where the samples were decidedly small, the results obtained show changes very similar to those found to take place in the Eden; that is, a very high value is reached soon after feeding commences in the first summer, and this is followed by a rapid fall; in the following spring there is a second maximum, again followed by a rapid fall. The second maximum is not so clearly shown by the Thurso data as by the Eden data; but the second maximum in the Eden was only of short duration, and it is possible that a more decided maximum occurred in the Thurso during the period between the

two collections made in March and June 1938. The actual values for quantity of food found in the Thurso system correspond closely with those obtained at corresponding times in the Eden. The general shape of these curves corresponds with those found by Ricker (1937) in *Oncorhynchus nerka*. In this species, however, the maximum stomach content is found later in the summer. It appears likely that in this case the shape of the food curve, particularly as regards the decrease in the autumn, is correlated with fluctuations in the food supply available and that this in turn affects the rate of growth.

Table 4. *The mean temperature of the water of each stream for each month during the period of the investigation*

	Temperature (°C.)		
Month	Sinclair Burn	Sleach Water	Halkirk Burn
Sept. 1937	10·2	9·8	10·5
Oct. 1937	9·3	7·7	9·0
Nov. 1937	3·0	4·0	4·5
Dec. 1937	1·1	1·2	2·2
Jan. 1938	2·7	2·4	3·6
Feb. 1938	2·0	2·4	3·0
Mar. 1938	6·8	6·2	5·9
Apr. 1938	6·0	7·0	6·4
May 1938	10·4	9·8	8·9
June 1938	12·5	12·0	12·2
July 1938	13·3	13·2	12·8
Aug. 1938	16·4	14·1	14·4
Sept. 1938	—	11·1	11·4

Table 4 shows for the period of the observation the monthly mean temperatures of the three streams studied. These monthly means which are based on daily readings taken at 9 a.m. are plotted in Fig. 2. It will be seen that, as in the Eden, rapid growth in length commences approximately simultaneously with the beginning of the rapid rise in temperature, and that the slowing down in growth commences while the temperature is still near its maximum.

It is possible that the seasonal changes in the quantity of food in the stomach and therefore in the rate of feeding may be the result of changes in the quantity of food available to the fish. It is desirable therefore to determine what seasonal changes take place in the fauna on which the fish feeds. In Table 5 are shown the mean number of animals per square foot in each of the streams studied on each occasion that a collection of fish was made there. These means are based on the results of two collections each of 2 sq. ft., taken in typical but contrasting substrata. The table shows the total number of animals, and also the number belonging to each of the four groups, *Ephemeroptera*, *Plecoptera*, *Trichoptera* and *Chironomidae*, which between them make up by far the greater part of the food of young salmon.

The results show clearly that there is no consistent seasonal change in the quantity of food available to the fish. The pronounced decline in the total number of animals belonging to the four food groups which took place in the

Sleach Water during the early part of the investigation appears to be due to the great decrease in numbers of *Chironomidae* which took place in this stream throughout the whole period of the investigation. It appears probable that this decrease was due to an epidemic or to some similar cause, and that therefore it should not be regarded as a seasonal change in numbers. Thus, in the Thurso system, as in the Eden, the seasonal changes which take place in the quantity of food in the stomachs, and in the rate of growth, do not appear to be due to changes in the quantity of food available.

Table 5. *The mean number of animals, of various groups, and of all forms, per square foot. Results for each stream and each group of collections given separately*

	1937		1938			
	27–31 Aug.	17–23 Nov.	18–21 Mar.	6–7 June	5 Aug.	3 Oct.
Sinclair Burn						
Ephemeroptera	2	3	12	7	2	2
Plecoptera	2	3	7	4	4	2
Trichoptera	1	8	6	4	3	5
Chironomidae	7	39	19	31	8	1
Total of above	12	53	44	46	17	10
Other animals	20	16	41	54	14	22
Total	32	69	85	100	31	32
Sleach Water						
Ephemeroptera	34	18	37	39	63	19
Plecoptera	54	67	26	11	12	80
Trichoptera	24	65	19	26	8	20
Chironomidae	236	91	31	31	17	3
Total of above	348	241	113	107	100	122
Other animals	275	260	193	176	275	163
Total	623	501	306	283	375	285
Halkirk Burn						
Ephemeroptera	35	13	86	91	99	66
Plecoptera	5	3	22	35	23	18
Trichoptera	49	12	22	22	31	72
Chironomidae	102	23	92	117	98	12
Total of above	191	51	222	265	251	168
Other animals	161	38	127	125	79	67
Total	352	89	349	390	330	235

As a result of the studies of the growth of young salmon in the river Eden certain hypotheses were put forward regarding the relation between various factors which showed seasonal changes. It was considered that 7° C. could be regarded as a critical temperature in the life history of the young salmon. Below 7° C. the fish appear to be lying quiescent in sheltered places, feeding very little, and making no growth. White (1939) also observed that during the winter young salmon in the Margaree river were lying quiescent and states: 'During winter conditions we have found the salmon parr only beneath stones.' No observations, however, are recorded concerning the exact period or temperature limits within which this applies. Simultaneously with the

rise of temperature above 7° C. in the spring the fish resume active life and begin to feed rapidly, and growth recommences. In the autumn the fall of the temperature below 7° C. appears to coincide with the disappearance of the fish from the open shallows, and with the cessation of all growth.

Comparison of the growth and temperature curves given in Fig. 2 shows that the data obtained in the Thurso system are in agreement with the hypotheses based on the Eden results. The efficiency with which fish can be netted depends to a considerable extent on their activity, and fish which are lying quiescent under the shelter of stones and overhanging banks are harder to capture. Consequently the number of fish netted in a standard length of water provides some indication of the extent to which the fish are active. The numbers of fish on which the mean sizes in Table 2 are based are the total numbers captured in each stream while netting the standard length. It will be seen that for both first-year and second-year fish the number captured during the winter conditions of November 1937 is very much lower than that taken in the summer conditions of August 1937, or of August 1938. In the Sinclair and Halkirk Burns the number of fish taken in March 1938 was again small, being in most cases even less than that taken in November 1937. In the Sleach Water, however, the number of fish taken was approximately the same as that taken in August 1937, and much higher than that taken in November 1937. Examination of the temperature records of the three streams shows that in the eight days prior to the date of collection the temperature of the Sleach Water had been between 7° C. and 8·5° C. on six occasions, whereas in neither of the other waters had temperatures higher than 6·5° C. been recorded at all up to the date of collection. These results also support the hypothesis that 7° C. is a critical temperature determining the activity and hence the feeding and growth of the young salmon.

As in the Eden, the rate of growth in the Thurso tributaries is less in the later part than in the early part of the summer. From the data available it is not, however, possible to determine whether the decrease in the rate of growth is gradual or whether there are two distinct periods of rapid and slow growth.

The seasonal variations shown by the condition factor of the young salmon of the Thurso system resemble in type those found in the Eden. In the first summer the condition factor rises rapidly until July, and from July until the end of the summer it remains constant at a high value. After a rapid decline in October and November it remains low during the winter. At the beginning of the second summer, at about the same time as the recommencement of growth in length, the condition factor begins to rise rapidly. As in the first year it continues to rise until about July, and from then till the end of the summer remains fairly constant. It again falls rapidly during October and November and remains low during the second winter. In the Sinclair Burn, where no growth was made by the second-year fish during the second part of the summer of 1938, the condition factor fell steadily from June until October.

In the other two streams studied, where growth continued slowly during this period, the condition factor rose slowly. In general, the results which have been obtained in the Thurso system support the hypothesis concerning the relation between rate of growth and condition factor, which was developed from the study of the growth of young salmon in the river Eden. This hypothesis was stated as follows: 'When growth is rapid condition is high; if at the beginning of the growth period condition is low growth in weight exceeds growth in length until condition has increased sufficiently. When growth is slow condition is poor, and if originally high is reduced by an excess of growth in length over growth in weight. When no growth is taking place condition declines to an even lower value.' In the Thurso system, however, there does not appear to be the decline in condition during the slow growth period which usually took place in the Eden. This phenomenon was not, however, invariably recorded in the Eden, particularly among second-year fish, and it is probable that its occurrence depends both on the condition of the fish at the commencement of the slow-growth period and the actual rate of growth during this period.

This hypothesis concerning the close relation between condition and rate of growth is further supported by a comparison of the three streams studied in the Thurso system. Table 2 shows that the condition factor of the young salmon of the Sinclair Burn is almost always much lower than that for the other two streams, and, as will be shown later, the rate of growth is very much less in this stream than in the Halkirk Burn and Sleach Water.

4. Discussion

From the observations which have been made in the Eden and Thurso river systems it is possible not only to study seasonal variations in the rate of growth, but also to compare the growth of young salmon in the different streams. In all cases the young fish are growing during a portion of the year only; therefore the total amount of growth made in each year depends both on the length of the growth period and on the rate of growth during this time. Table 6 shows for all the streams studied the increase in length in each of the first and second years. It also shows for each year the average rate of growth during the period from June to August. Of those periods for which data were available from the Thurso system, the period June to August was selected as corresponding most nearly to the rapid growth period. In the Thurso system the data for the first year are provided by the 1938 year class, and for the second year by the 1937 year class. In the Eden system data are given for the 1935, 1936, and 1937 year classes. In calculating the annual increment of length during the first year a mean length at hatching of 2·5 cm. has been assumed in all cases.

The variations in the rate of growth during the first year shown by the different year classes in the river Eden probably arise from the fact that the

growth rates had to be calculated for slightly different periods in the different years. The table shows that the rate of growth in the first year differs considerably among the streams of the Thurso system, and that in both the first and second years the rate of growth in the Halkirk Burn is markedly greater than in the other two streams. In both years the rates of growth found in the Eden are somewhat less than those of the Halkirk Burn. The annual increments in the Eden are, however, consistently rather greater than in the Halkirk Burn and considerably greater than in either of the other Scottish streams.

Table 6. *The total annual growth and the growth rate for the period June to August in each of the first two years. Results for the three Thurso streams and for three year classes in the Eden given separately.*

	Sinclair Burn	Sleach Water	Halkirk Burn	Eden 1935	Eden 1936	Eden 1937
First year:						
Initial length (cm.)	2·5	2·5	2·5	2·5	2·5	2·5
October length (cm.)	4·5	5·9	7·3	7·4	7·4	8·0
Annual increment (cm.)	2·0	3·4	4·8	4·9	4·9	5·5
June length (cm.)	3·21	3·34	3·85	4·5	4·9	4·3
August length (cm.)	4·13	5·22	6·25	6·5	6·5	5·7
Increment (cm.)	0·92	1·88	2·40	2·0	1·6	1·3
Interval (days)	59	58	60	63	48	34
Rate (cm./day)	0·016	0·032	0·040	0·032	0·033	0·038
Calculated growth period (days)	125	106	120	153	149	145
Second year:						
Initial length (cm.)	4·75	6·95	6·6	7·4	7·8	—
October length (cm.)	8·2	11·5	12·45	13·5	13·7	—
Annual increment (cm.)	3·45	4·55	5·85	6·1	5·9	—
June length (cm.)	6·2	9·1	9·4	10·1	11·1	—
August length (cm.)	8·1	11·15	11·8	12·8	12·6	—
Increment (cm.)	1·9	2·05	2·4	2·7	1·5	—
Interval (days)	59	58	60	77	42	
Rate (cm./day)	0·032	0·035	0·040	0·035	0·036	—
Calculated growth period (days)	108	130	147	175	164	—

The results suggest that there is a significant difference between the length of the growth period in the two areas studied; and an arbitrary determination of this period, which, although it is not identical with the actual growth period, will enable comparisons to be made between different waters, can be obtained by dividing the annual increment by the rate of growth during the June to August period. Table 6 shows that the growth period as measured in this way is consistently considerably longer in the Eden than in any of the Thurso streams. The particularly short growth period calculated for the second year in the Sinclair Burn is probably due to the very small amount of growth which takes place in this stream during what is normally the slow growth period from August to October.

From the data given above it would appear that both the rate of growth and the length of the growth period play a significant part in determining the

actual amount of growth which is made in the various streams studied. It has already been shown that the commencement of growth in the second year is determined by the time of the rise of temperature to 7° C., and it appears possible that this factor may be at least partly responsible for the differences found in the calculated growth periods in the two river systems. Table 7 shows the dates on which growth would have commenced in the different streams if it had continued steadily at the rates given in Table 6 from the time of commencement in the spring until the time of collection in August. The initial lengths and August lengths used are the mean lengths found to occur during the previous winter and at the time of collection respectively. The table also shows in each case the date on which the temperature first rose permanently to 7° C. It will be seen that the mean value of these two dates show for the two river systems a strikingly similar relationship. The length of the calculated growth period shown in Table 6 depends, however, not only on the date of commencement of growth in spring, but also on the date of commencement

Table 7. *The calculated date of commencement of growth in the second summer compared with the date of the rise of temperature to* 7° C. *Results for the three Thurso tributaries and two Eden year classes given separately*

	Thurso				Eden		
	Sinclair Burn	Sleach Water	Halkirk Burn	Mean	1935	1936	Mean
Aug. length (cm.)	8·1	11·15	11·8	—	12·8	12·6	—
Rate (cm./day)	0·032	0·035	0·040	—	0·035	0·036	—
Initial length (cm.)	4·75	6·95	6·6	—	7·4	7·8	—
Aug. date	9 Aug.	6 Aug.	5 Aug.	—	11 Aug.	23 Aug.	—
Calculated initial date	26 Apr.	8 Apr.	28 Mar.	10 Apr.	9 Mar.	12 Mar.	10 Mar.
7° C. date	22 Apr.	20 Apr.	21 Apr.	21 Apr.	18 Mar.	8 Apr.	28 Mar.

and the duration of the subsequent slow growth period, and on the actual rate of growth during this time. In Table 8 the rate of growth during the period August to October is shown and compared with that during the period June to August. The variation between the different streams in the rate of growth is greater in the slow growth period than in the rapid growth period. The order of the three Thurso streams as regards rate of growth in the later period, i.e. Sinclair Burn, Sleach Water, Halkirk Burn, is, however, the same for both years as in the case of the rapid growth period. The rate of growth in the Eden during this period appears to be slightly greater than that found in the Halkirk Burn.

When comparison is made of the rates of growth in the rapid and slow growth periods, it appears that in the first year the relation does not vary greatly between the different streams, but that in the Eden the rate of growth in the second period is relatively slightly greater than in the Thurso streams. In the second year, however, there is great variation in the ratio between the two growth rates, although in this case also growth during the slow growth period is relatively greater in the Eden than in the Thurso streams. It is clear

that considerable variations may occur in the duration and intensity of the slow growth period. On the data at present available it does not appear possible to assign a cause either to the slowing down of growth in late summer, or to the variations which occur in this phenomenon. The data suggest, however, that salmon are not altogether similarly affected in their first and in their second years by the phenomena which control this reduction in growth rate.

Among the possible causes of this reduction in late summer are a reduction in the amount of food available at this time, and the effect of high temperatures during the summer. Table 8 gives the ratio between density of the fauna during the slow growth period and during the rapid growth period. The ratio

Table 8. *Comparison of growth rates for June–August and August–October, related with temperature and changes in fauna. Results for the three Thurso tributaries and for three year classes in the Eden given separately*

	Sinclair Burn	Sleach Water	Halkirk Burn	Eden 1935	Eden 1936	Eden 1937
First year:						
Aug.–Oct. increment (cm.)	0·37	0·68	1·05	—	0·9	2·3
Interval (days)	55	56	56	—	58	87
Rate (cm./day)	0·007	0·012	0·019	—	0·016	0·026
June–Aug. rate (cm./day)	0·016	0·032	0·040	—	0·033	0·038
June–Aug. rate / Aug.–Oct. rate	2·3	2·7	2·1	—	2·1	1·5
Max. temp. (° C.)	24·0	19·75	18·5	—	18·0	18·5
Degree-days above 18° C.	37	6·5	1	—	5	1
Aug.–Oct. fauna / June fauna	0·31	1·04	0·80	—	1·68	1·68
Second year:						
Aug. –Oct. increment (cm.)	0·10	0·35	0·62	0·7	1·1	—
Interval (days)	55	56	56	58	87	—
Rate (cm./day)	0·002	0·006	0·011	0·012	0·013	—
June–Aug. rate (cm./day)	0·032	0·035	0·040	0·035	0·036	—
June–Aug. rate / Aug.–Oct. rate	16·0	5·8	3·6	2·9	2·8	—
Max. temp. (° C.)	24·0	19·75	18·5	18·0	18·5	—
Degree-days above 18° C.	37	6·5	1	5	1	—
Aug.–Oct. fauna / June fauna	0·31	1·04	0·80	1·68	1·68	—

given is that between the total numbers per square foot of the four groups *Ephemeroptera*, *Trichoptera*, *Plecoptera* and *Chironomidae*. For the rapid growth period the density used is the mean for June collections; for the slow growth period the mean September values have been used in the Eden, and the mean of the August 1938 and October 1938 values in the Thurso system. It is interesting to observe that the exceptional slowing down in growth which occurs in second-year fish in the Sinclair Burn is associated with a great reduction in the fauna of this stream in late summer. On the other hand a marked reduction in growth rate also occurs in the Eden, where there is actually an increase in the abundance of the fauna.

Table 8 also shows for each stream the maximum temperatures recorded during the summers under consideration, as well as the total number of degree-

days above 18° C. during this time. It will be seen that in the Thurso streams both these values appear to show some association with the intensity of the reduction in growth rate in the case of second-year fish. In the case of first-year fish, however, no such correlation is apparent. These facts suggest that neither reduction in food supply nor high temperatures are the primary cause of the reduction in the rate of growth although it is possible that either of them may influence its extent. Whatever its cause, the reduction in the rate of growth during late summer plays an important part in determining the total amount of growth made in each year.

It is seen that the annual increment in length depends partly on the duration of the growth period, and that this is determined at least to some

Table 9. *The dimensions of the regular netting areas in the three Thurso tributaries and the Eden (Ousen Stand); also the average number and weight of fish caught in each of these*

	Sinclair Burn	Sleach Water	Halkirk Burn	Eden Ousen Stand
Length (m.)	1100	870	305	565
Breadth (m.)	2·5	4·25	2·75	29
Area (hect.)	0·27	0·37	0·084	1·64
No. of fish caught:				
Salmon	115	94	92	80
Trout	320	150	4	82
Total	435	244	96	162
Weight of fish caught (kg.):				
Salmon	0·30	0·70	0·60	1·61
Trout	2·02	6·84	0·11	6·94
Total	2·32	7·54	0·71	8·55
Weight of fish caught (kg.) per hect.	8·6	20·4	8·4	5·2
Available fauna (no./sq. ft.)	80	294	300	454
Fauna density / Fish density	9·3	14·5	35·7	87·6

extent by climatic factors. The annual increment also depends, however, upon the rate of growth during the rapid growth period and it has been shown that this may vary considerably in different streams. Wide variations in the rate of growth in adjacent streams for the same period are unlikely to be produced by climatic factors, and it appears possible that in this case the rate of growth is controlled to some extent by the quantity of food available to the fish. Table 9 shows the dimensions of the area studied at the Ousen Stand station on the river Eden and in each of the three streams of the Thurso system. The table also shows the average number and weight of fish taken in a complete netting of each of these stations. In order that the figures given may be as complete as possible the results used are those obtained in the autumn when the fish hatched in the preceding spring are sufficiently large to be netted with fair efficiency and when the quiescent period has not yet commenced. The results given for the Thurso stream are those obtained in late August 1937 and the Eden results are the average yield of a number of nettings carried out in October 1936 and October 1937.

In all the streams investigated salmon and trout made up by far the greater part of the fish present, although in the Sleach Water and the Halkirk Burn sticklebacks (*Gasterosteus aculeatus*) occurred in small numbers, while in the Eden a number of species including minnows (*Phoxinus phoxinus*), grayling (*Thymallus thymallus*) and chub (*Leuciscus cephalus*) were occasionally taken. The minnow is actually fairly abundant in the Ousen Stand reach of the Eden, but generally inhabits regions of slack water not occupied by Salmonoid fishes. The total weight of fish actually netted in each stream is given in kilograms per hectare. Since it is impossible in a reasonable time to net all the fish in any reach of a stream these figures do not represent the actual densities of the fish populations. An experiment was therefore undertaken in August 1938 to determine the efficiency of the netting methods used in the Sinclair Burn. The area under observation was netted in the usual way and a number of salmon of each of the three year classes present were captured, marked by the removal of the adipose fin, and liberated. On the following day the area was again netted, and a number of salmon, both marked and unmarked, were captured. The results are given in Table 10 and from them the approximate efficiency of the netting methods used can be calculated.

Table 10. *Estimation of efficiency of netting. Results obtained in the Sinclair Burn, August*, 1938

Year class	No. of fish marked	No. taken in 2nd netting	No. of marked fish recaptured	% marked fish recaptured
1938	48	46	10	21
1937	25	18	7	28
1936	8	6	4	50
Total	81	70	21	26

It will be seen that there is a progressive increase in the efficiency of the methods with the age of the fish. This is probably due to the fact that it is relatively easier for smaller fish to lie among the stones of the bottom and allow the nets to pass over them. All the Thurso tributaries studied are comparatively small and the same gear was used in all of them. It is therefore probable that the efficiency of the netting was approximately the same in each case, and that the results shown in Table 9 represent between one-quarter and one-third of the actual densities of fish present in these streams. Owing to the much greater size of the river Eden and the different type of gear used it is not possible to estimate from the Sinclair Burn results what correction should be applied to the Eden figures. It is probable, however, that the efficiency of the netting was considerably less in the Eden than in the Thurso tributaries.

Table 9 also shows the average density of the available fauna in the different streams studied, as determined by the methods previously described (Allen, 1941). The density of the available fauna in numbers per square foot, when divided by the density of the fish population in the units used (kg. per

hect.), provides an arbitrary measure of the abundance of the food supply in relation to the fish population. It is noticeable that the order of the three Thurso tributaries as regards the relative abundance of food supply is the same as for the rate of growth of the young salmon during the rapid growth period. The relative abundance of the food supply as determined in this way is very much higher in the Eden than in any of the Thurso tributaries; but it is probable that this arises from the relative inefficiency of the netting carried on in this stream. These results appear to give considerable support to the hypothesis that the quantity of food available is in this instance a major factor in determining the rate of growth of the young salmon during their rapid growth period.

Studies of the growth of salmon based on the scales of adult fish have shown that not only the age at migration but also the rate of growth during freshwater life are correlated with latitude. The correlation is positive in the former case and negative in the latter. It has already been shown that a climatic factor—the rise of temperature in the spring, which tends to vary with latitude, may affect the amount of growth made by young salmon during each summer by determining the length of the growth period. It is therefore desirable to examine the extent to which this factor may be responsible for the correlation between rate of growth and latitude. For this reason the geographical distribution of the date at which the temperature rises above 7° C. in the spring and of the annual increment made by young salmon during their second year have been compared. This comparison has been extended over as great a part of the natural range of the salmon as possible.

Table 11 shows for a number of rivers or districts the calculated average lengths of salmon at the end of their first and second years, and the increase in length made during the second year. In calculating the average length at the end of the first year only those fish have been included which completed at least two years in fresh water before migration to the sea. Belding (1936) has shown that, for a given population of salmon, different values for the calculated average lengths at the ends of the different freshwater years are obtained from the scales of smolts and from the scales of adult salmon. For this reason comparisons of the growth of salmon in different rivers must be based only on cases in which the growth has been determined from the same type of material. Since many more growth determinations have been based upon the examination of the scales of adult salmon than upon other types of material, the data given in Table 11 have all been obtained in this way. While these results do not represent accurately the actual growth in these waters, the error is probably similar in all cases, and the figures can legitimately be used for purposes of comparison. Fig. 3 shows, on the same map, the annual increment during the second year in the various waters and the position of the 45° F. (7·2° C.) isotherm for each of the first six months of the year (Buchan, 1899; Shaw, 1928).

It will be seen from this figure that, within the restricted area of the British Isles, there is a clear relation between the position of the isotherm and the rate of growth. With few exceptions the April isotherm separates the rivers in which the annual increment exceeds 6 cm. from those in which it is less than 6 cm. When, however, the data for the British Isles are compared with the somewhat meagre data available from Scandinavia and North America the correlation no longer applies. In both these areas more growth is made during the

Table 11. *The growth of salmon during the second year in various rivers and districts as calculated from the scales of adult fish*

River or district	Length after 1st yr. cm.	Length after 2nd yr. cm.	Increment cm.	Source of data
British Isles:				
Balgy	3·4	8·2	4·8	Nall (1928)
Ballisodare	4·6	10·9	6·3	Went (1941)
Conon	3·5	8·7	5·2	Menzies (1928)
Dee (Aberdeen)	3·9	9·5	5·6	Menzies (1922); Menzies & Macfarlane (1924*b*, 1926*a*, 1927*a*, 1932)
Dee (Kirkcudbright)	4·5	12·0	7·5	Macfarlane (1931)
Don	4·8	10·5	5·7	Menzies (1923*b*)
Ewe	5·1	10·7	5·6	Nall (1933)
Findhorn	4·4	10·3	5·9	Menzies (1923*b*)
Forth	4·6	10·9	6·3	Menzies 1923*b*)
Grimersta	3·9	8·8	4·9	Menzies (1927)
Hope	3·9	9·0	5·1	Nall (1927)
Nith	5·5	13·7	8·2	Macfarlane (1936*b*)
Shannon	5·5	14·2	8·7	Southern (1928); Went (1938)
Shiel	5·0	10·1	5·1	Nall (1928)
Spey	4·0	9·6	5·6	Menzies (1923*a*); Menzies & Macfarlane (1924*a*, 1926*b*, 1928 *a* and *b*)
Tay	3·7	9·7	6·0	Macfarlane (1934, 1936*a*)
Tweed	4·9	12·0	7·1	Menzies (1923*b*); Macfarlane (1933*a*, *b*)
Ullapool	3·9	9·9	6·0	Nall (1928)
Upper Solway (Annan)	5·3	13·7	8·4	Macfarlane (1938)
Scandinavia:				
Northern Baltic	4·2	9·8	5·6	Dixon (1934)
Norrbotten	4·0	9·2	5·2	Rosén (1918*a*)
Västerbotten	4·4	11·4	7·0	Rosén (1918*b*)
North America:				
Grand Cascapedia	4·2	9·5	5·3	Calderwood (1927)
Moisie	3·9	8·9	5·0	Menzies & Macfarlane (1927*b*)
Newfoundland, West coast	3·8	7·8	4·0	Belding (1936)

second year than would be expected from comparison with the British results. Thus, while the date of the rise of temperature to 7° C. may affect the annual increment in length within restricted areas by determining the date of the commencement of growth, some other factor must be sought to explain the variations found in the rate of growth in different parts of the range of salmon. It is possible that the lower summer temperatures in high latitudes produce a less pronounced slowing down in growth in late summer, and that this compensates for the later commencement of growth in the spring.

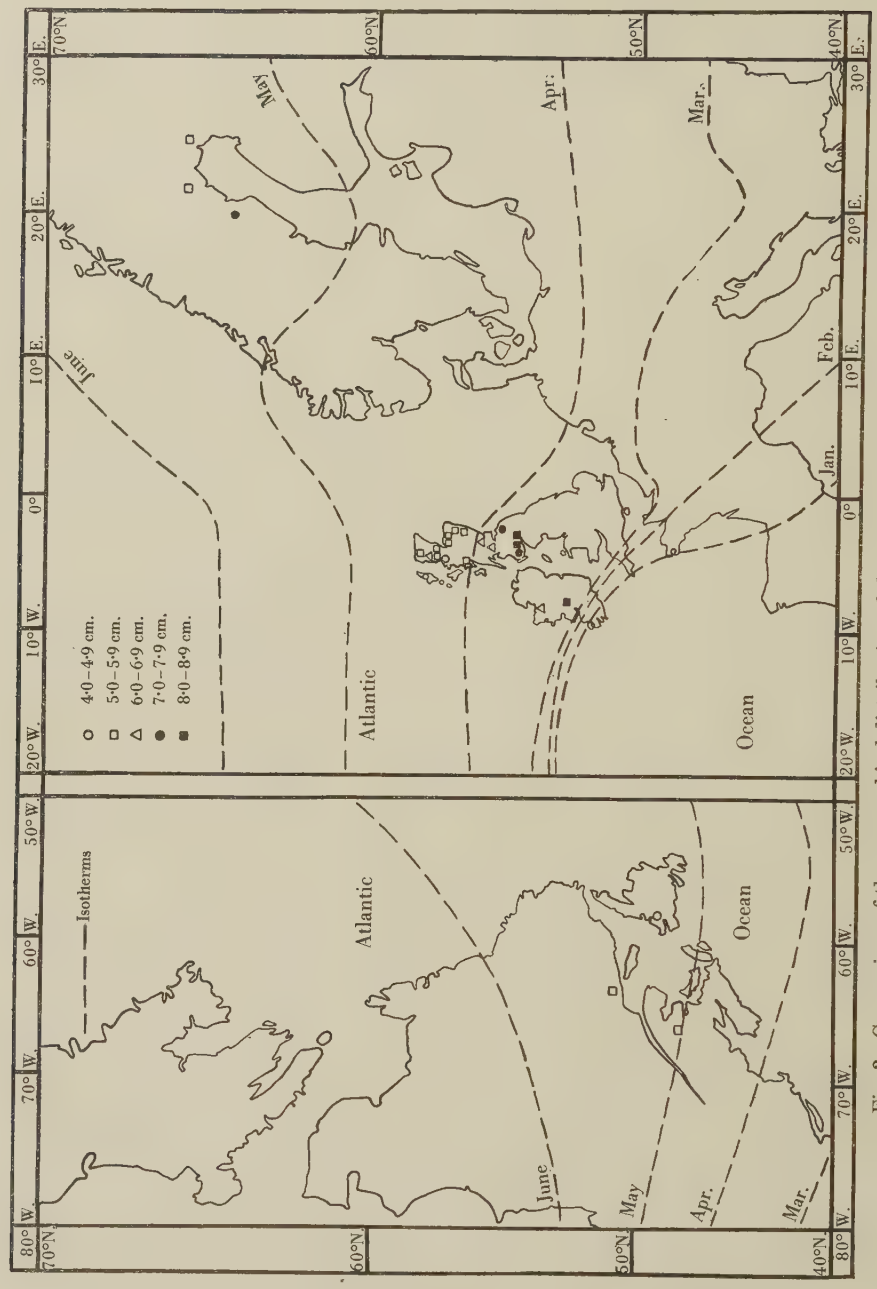

Fig. 3. Comparison of the geographical distribution of the second-year increment in the growth of salmon with the 45° F. (72° C.) isotherm for the first six months of the year.

The above comparison has been based on the growth made during the second year, since the hypothesis regarding the effect of temperature upon the time of commencement of growth cannot apply to the first year. It is probable, however, that similar effects will be shown in the first year, since the time of hatching of the fry is determined by the temperature of the water during the period of incubation.

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6. Summary

1. A study of the growth of young salmon in three tributaries of the Thurso river, Caithness, was carried out between August 1937 and October 1938. These results are compared with those from a similar study of the young salmon of the river Eden, in Cumberland and Westmorland.

2. The seasonal variations in the growth-rate and related phenomena in the Thurso system correspond extremely closely with those from the Eden.

(*a*) Growth takes place during only a part of the year; the growth period, April to September, is slightly shorter in the Thurso system than in the Eden.

(*b*) Growth is slower in the later part of the summer than in the early part.

(*c*) The amount of food found in the stomachs of the salmon is at a maximum during the early part of the rapid growth period in both first and second years, and then falls steadily to a low value at which it remains during the winter.

(*d*) The seasonal changes in the condition factor of the fish may be correlated with changes in the rate of growth. When condition is good the rate of growth is high and when condition is poor the rate of growth declines or remains low.

3. Further evidence is produced in support of the hypothesis that the temperature 7° C. is critical in determining the activity and hence the feeding and growth of young salmon.

4. The mean rate of growth in the second year for the period June to August is calculated for the three Thurso tributaries and for the Eden, and from this a theoretical date of commencement of growth is obtained. This date is considerably later in all the Thurso tributaries than in the Eden, and the difference is similar in extent to the difference between the average dates of the rise of temperature to 7° C. in the two systems.

5. Division of the total annual increment by the June to August growth-rate indicates that the total length of the growth period in both first and second years is less in the Thurso system than in the Eden.

6. The order of the streams studied is the same in respect to the rate of growth during the slow growth period, August to October, as to the rate of growth from June to August. The ratio between the rates of growth during these two periods shows that it is similar in the different waters in the first year but varies widely in the second year. In both years the rate of growth during the slow growth period is relatively higher in the Eden than in the Thurso tributaries.

7. While either the maximum summer temperatures or seasonal variations in the fauna may in some cases affect the extent of the decrease in the rate of growth in late summer neither is the primary cause.

8. The order of the streams is the same in regard to the relation between the food supply and the fish populations as in regard to the rate of growth during the rapid growth period.

9. The amount of growth in one year depends on:

(*a*) The amount of food available, which affects the rate of growth during the rapid growth period.

(*b*) The date of the rise of temperature to 7° C. which determines the date of commencement of rapid growth.

(*c*) The unknown factors which determine the length of, and the rate of growth during, the slow growth period.

10. Comparison between the second year increment and the date of the rise of temperature to 7° C., throughout the natural range of the salmon, shows that while this factor may affect the annual increment within restricted areas, some other factor is of greater significance in determining its magnitude in different parts of the range.

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THE AMPHIPOD FAUNA OF OLDANY HARBOUR, SUTHERLAND

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(With One Figure in the Text)

1. General description

Oldany Harbour is situated behind Oldany Island on the south shore of Eddrachillis Bay on the west coast of Sutherland. The harbour is used almost solely by the boats of a few lobster fishers and that only in the winter. At one time it probably afforded safe anchorage to quite a number of boats engaged in the lobster, herring and white fish industries. The reduction in numbers of the latter and the dwindling population of fishermen have led to the disuse of the harbour. With the exception of a small stone jetty no attempt has been made to provide a landing place. Such, however, is hardly necessary since the rocky coast is admirably suited for the approach of small boats.

From this harbour there are two exits (see Fig. 1). The south channel (B) leads directly westward from the basin (C) in which at low water of ordinary spring tides there is some $1\frac{3}{4}$ fm. of water. The channel, however, dries out for a short distance at its inner end at springs. This channel leads to the sea through Clashnessie Bay (A) which is sheltered from the prevailing south-west winds by the long headland of Rhu Stoer and from the north by Oldany Island. To leave by the north channel a boat has to pass through the lagoon, which at low water of ordinary spring tides has a maximum depth of only $\frac{1}{4}$ fm. The final exit to the sea is then by a very twisted, narrow and rocky channel through which (as also in the case of the south channel) the tide races with considerable speed. This channel, however, never dries. The lagoon is filled by water entering through the north channel, while the basin receives its water through the south channel. Owing to the narrowness of the channels and to the height of the surrounding land, the water is very little affected by wind from any direction. It is therefore a very suitable habitat for a great many species which do not occur in the more exposed water outside. The coasts of the basin and lagoon show an immense variety of habitats.

Since the adjacent land is composed of gneiss the cliffs tend to be smooth and vertical and are of the very permanent type (**10**). Where the shore is composed of boulders or shingle the pieces are mostly of gneiss, Torridonian fragments and to a lesser extent Cambrian quartzite, of which the last two at least have been transported by ice. A great many of the massive cliffs, however,

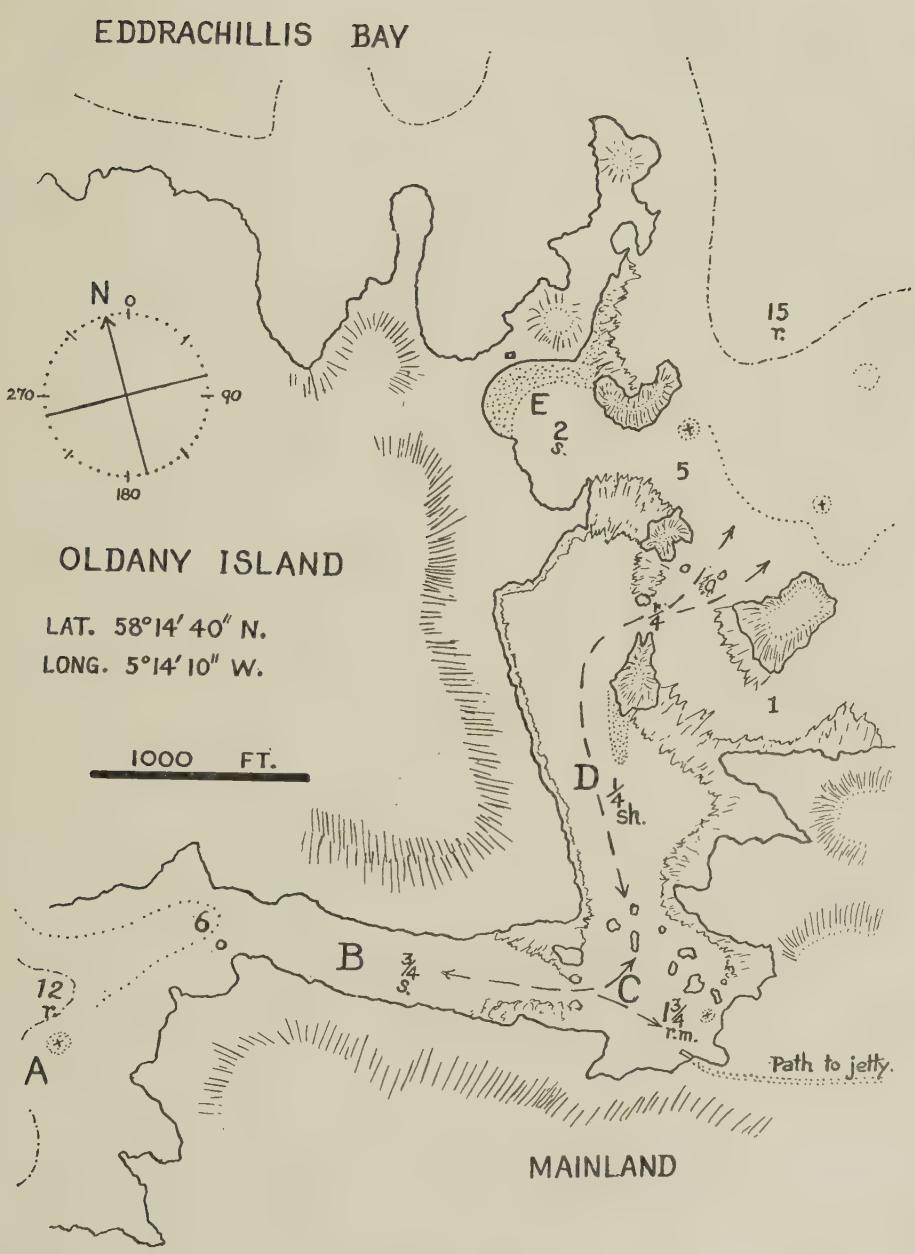

Fig. 1. Sketch map of Oldany Harbour, Sutherland. A, Clashnessie Bay; B, South Channel; C, Basin; D, Lagoon; E, Sands. Depth in fathoms. Arrows indicate direction of tidal ebb and flow. *s.* sand; *sh.* shelly sand; *r.* rock; *m.* mud.

do not always present smooth surfaces, despite their origin: they may be cracked or fissured owing to the pressure to which the rock has been subjected in the past and to the heat of later intruded masses.

There are no streams breaking the coastline, so the question of an estuarine fauna does not arise. Such fresh water as drains off the land into this particular part of the sea does so by seepage through the peat or as small temporary torrents falling almost vertically down the cliffs. On the shelf in front of the gneissose cliff and in the inlets and gullies there is a belt which may be composed of boulders, shingle or mud. The water area between the two channels is clearly divided into two very distinct parts by a line of rocky islets, covered at high water of spring tides, which also limit the tidal flow (Fig. 1), except just below low water of spring tides, when the south channel dries and a small quantity of water passes from the basin into the lagoon.

The nature of the floor of the basin and of the lagoon are markedly different. The basin is the smaller in area. Its shores are of shingly or bouldery mud which ends abruptly and passes sharply down into a floor of the same type, where the large boulders are largely the jettisoned ballast of many long-passed fishing-boats. Owing to these boulders it is a difficult place in which to use a dredge or trawl. The shore of the lagoon, though of the same general type, passes gently into the floor, which is completely different in type. It is composed almost entirely of broken shell free from stones or boulders. While the north shore of the south channel is steep-to, that of the south shore is largely composed of boulders. The floor is mostly of bouldery or shingly mud supporting a large number of seaweeds, of which the most obvious, as it is swept to and fro by the strong tides, is *Chorda* sp. It is not difficult to use a dredge in this channel since, despite the speed of the current, the channel is straight and wide enough to allow a boat in difficulties to be kept off the shore. In this respect the south channel compares very favourably with the north channel. In it dense beds of *Laminaria* sp. cover a floor of sharp rocks over which the boat has to travel through a fast and turbulent current along a narrow and twisting passage on its way to open water. Needless to say, dredging is not easily nor safely carried out under such conditions.

The only beach of sand stretching from below to above tidemarks is in a well-sheltered bay (Fig. 1, E) just beyond the north channel. This sand rises sufficiently high to form an isthmus between Oldany Island and a small rocky headland. The sand of this bay contains a fair percentage of non-calcareous particles.

2. Analysis of sands

The *shore sand* differs very markedly from that of the lagoon floor. Mechanical analysis of the shore sand shows it to be of very even particle size, with only 0·2 % having a diameter of more than 0·50 mm., and all the rest lying between 0·50 and 0·1 mm. There is a complete absence of silt or

fine shingle, The actual analysis is given below in cumulative percentages. This sand contains 76·6 % of broken shell.

Size of particle mm.	Cumulative percentage
0·50	0·2
0·25	35·0
0·232	50·0
0·20	75·5
0·10	100·0

The *lagoon sand*, on the other hand, has a much higher percentage of calcareous matter. It also contains a higher percentage of organic matter than is usual in shore sands, since these are subjected to wave action, while the floor of this particular lagoon is not subjected to any wave action at all. The analysis of a sample shows it to be made up as follows:

	%
Calcareous matter	83·6
Organic matter	2·5
Other matter	13·9

The last is composed of particles which are considerably larger than those of the shore sand. Although the size of the particles of the calcareous matter varies through a large range, the greatest number have an area of about 2 sq. mm. (It will be realized, of course, that these particles, being often plate-like and containing air-spaces, cannot be dealt with satisfactorily by an elutriator. Direct measurement has been used.)

Non-calcareous particles

Size of particle mm.	Cumulative percentage
1·3	96·0
1·1	53·4
0·50	30·4

A comparison of the tables of size of the non-calcareous particles shows very clearly the difference in the amount of wave action on the shore and on the floor of the lagoon, the average size of the grains being 0·232 mm. and 1·1 mm. respectively. The quantity of calcareous matter in this sand (83 %), though high, is not exceptionally so. The shell-sand beaches of Cornwall, for instance, have between 50 % and 90 % calcareous matter. A comparison of this shore sand with that of other beaches shows one or two interesting points. It is, for instance, much finer than sand from Port Erin beach. Of Oldany sand only 0·2 % has a diameter greater than 0·5 mm. whereas much of that of Port Erin reaches a diameter greater than 6 mm. (**9**). Boswell (**2**) gives a list of some 30 shore and blown sands the great bulk of whose particles lies between 0·25 and 0·5 mm. An analysis of a north coast sand from Rispond, Sutherland (**1**) shows that only 1·5 % of the grains have a diameter greater than 0·40 mm., and that the greatest bulk of the sand lies between 0·23 and 0·35 mm., with a sudden falling off in both directions. Thus it would seem that the Oldany

sand is a typical shore sand. The lagoon sand is interesting in that it has a large proportion of organic matter. This, of course, is of considerable importance to the fauna but, since it is much broken up, only to a fauna of burrowing filter or sieve feeders (**5**).

The shore sand is never subjected to more than a mild wave action so that it is little disturbed. Therefore, as might be expected, it supports a large fauna of *Talorchestia deshayesii*. These animals make shallow burrows and in so doing heave up little mounds until that particular part of the shore is dotted with them.

3. The fauna

(*a*) *The Amphipoda of the lagoon*

The sandy floor of the lagoon, over which great numbers of hermit-crabs crawl in their shells encrusted with *Hydractinia echinata* Fleming, supports abundance of burrowing Amphipods of the following species:

Bathyporeia guilliamsoniana	Urothoe elegans
Ampelisca spinicarpa	Urothoe marina

A good many more species are found living on such weeds as have managed to find attachment. These species are:

Cheirocratus sundvalli	Gammarus locusta
Corophium bonelli	Microprotopus maculatus
Corophium crassicorne	Pleonexes gammaroides
Dexamine spinosa	Siphonectes dellavallei
Ericthonius braziliensis	

(*b*) *The Amphipoda of the basin*

The basin, with its deeper water, muddy floor and smaller water movement, has a very different Amphipod fauna. As hermit-crabs might be called the characteristic animal of the lagoon, so *Ascidia mentula* O. F. Müller, whose large red bodies festoon every rock and boulder right up to the limit of low water mark of ordinary spring tides, is undoubtedly the characteristic animal of the basin. No other organism there catches the eye and imprints itself on the memory like this Ascidian, whose test and epiphytic growths afford a safe habitat for an abundance of Polychaetes, Isopods and other small crustaceans.

The Amphipods found in the basin are the following 12 species:

Ericthonius braziliensis	Amphithoe rubicata
Lembos websteri	Aora typica
Leucothoe spinicarpa	Coremapus sundvalli
Melita obtusata	Corophium acherusicum
Nannonyx goesi	Corophium bonelli
Orchemene humilis	Sunamphithoe pelagica

The mud which fills many of the inlets or 'goes', and forms the eastern shore of the basin, has no very representative fauna. *Gammarus marinus* is common, but is always associated with the stones which lie on the mud. When

a specimen of *G. marinus* from such a locality is compared with a specimen from the open shore some very minor variations are noticeable. There is, for instance, a tendency to narrowness in the basal joints of the pereiopods. This suggested that it might be worth comparing specimens of *G. marinus* from the north of Scotland with those of the south of England, in order to discover if any real quantitative difference existed between them, as suggested by Dr J. S. Huxley in his Clines Theory (**7**).

(*c*) *Size variations*

It was first decided to see if a length-weight ratio could be established. However, owing to the frequency of missing appendages or of abnormal regenerations, combined with the difficulty of making really accurate measurements it was decided to abandon this method. Then several specimens of about the same size from each locality were dissected and the proportions of the various parts compared. This was done by projecting one part, say a limb, on to a piece of bristol board and tracing its outline. Then the corresponding part from several specimens was superimposed by the same means on the sketch. Of course, the later specimens were brought to the same general size by alteration of the apparatus. By this means it was found that the amount of variation of normal (not regenerated) parts was very slight and worked out at a maximum for the 7th pereiopod of 0·25 mm. on a total limb length of 5·0 mm. This amount of variation, however, was as great between specimens from the same locality as between specimens from the south and the north. Naturally, of course, this does not disprove the Clines Theory, since between these two localities there is no barrier, so that there must be a flow, albeit a very slow one, of genes. It is perhaps worth noting that such variation as occurred in a limb was seldom spread evenly over all the joints but was most often associated with the length of the distal one, or less often the proximal. The middle joints tended to greater constancy.

The variation in form of specimens from both ends of Britain having been examined and found to show no significant differences, it is possible to examine another side of the case. Though proportions may remain constant, it is possible that habitats may alter. That such habitat alteration does occur in the Amphipoda has been pointed out by Goodhart & Harrison (**6**), who collected southern off-shore specimens from the intertidal regions of the north. This is a clear-cut distinction. Other habitat variation may be less obvious though of no less significance.

(*d*) *Habitat and community differences*

To make a comparison of the various habitat-types is not easy because it means depending on fauna lists and consulting records many of which are useless owing to their lack of precision.

The table gives a list of the Amphipod fauna of Oldany Harbour with the habitat of each species. In the third column is a list of other habitats, taken, where possible, from the *Plymouth Marine Fauna* (**8**), *Faune de France* (**3**) and from Crawford (**4**). When the habitat is similar in all localities it is so indicated.

Species	Oldany habitat	Other habitats
LYSIANASSIDAE		
Nannonyx goesi Boeck	On *Ascidia mentula* O. F. Müller	Low water (**8**)
Orchemene humilis (A. Costa)	On *A. mentula*	0–9 m., sand (**3**)
Orchemenella nana (Kröyer)	In dead crab	Similar
AMPELISCIDAE		
Ampelisca spinimana Chevreux	In sand, L.W.S.T., lagoon	15–20 m. in mud (**3**)
A. typica (Bate)	In sand, L.W.S.T., lagoon	Shelly gravel, Eddystone (**8**). L.W.M. Jersey to 77 m. Corsica (**3**)
HAUSTORIIDAE		
Bathyporeia guilliamsoniana (Bate)	In sand, lagoon	Similar everywhere
Urothoe elegans Bate	In muddy shingle and in clean sand	Shelly gravel (**8**): L.W. (**3**)
U. marina Bate	In clean sand	L.W. in sand (**3**)
PHOXOCEPHALIDAE		
Harpinia crenulata Boeck	Under stones on muddy gravel, L.W.N.T.	L.W. Roscoff; 10–30 m. in mud, le Croisic; 20–40 m., Ajaccio (**3**)
H. antennaria Meinert	Muddy gravel, 1½ fm.	In mud, 19 m., Concarneau (**3**)
AMPHILOCIDAE		
Gitana sarsi Boeck	In *Laminaria* holdfast	L.W. to 80 m. (**3**)
LEUCOTHOIDAE		
Leucothoe spinicarpa (Abildg.)	On *Ascidia mentula*	On ascidia (**3**)
CALLIOPIIDAE		
Apherusa jurinei (M. Edw.)	In *Halichondria*; under stones on muddy sand	Similar everywhere
GAMMARIDAE		
Cheirocratus sundvalli (H. Rathke)	On weed on sand, lagoon	Similar (**8**)
Melita obtusata Montagu	On *Ascidia mentula*	—
Gammarus marinus Leach	On *Ascophyllum*	Usually on *Fucus*
G. finmarchicus Dahl	In rock crack at half-tide	—
G. obtusatus Dahl	On *Ascophyllum*	—
G. locusta (L.)	On weed on sand, lagoon	On weed, under stones (**8**)
DEXAMINIDAE		
Dexamine spinosa (Montagu)	On weed on sand, lagoon	Similar (**8**)
D. thea Boeck	On weed, L.W.S.T.	—
TALITRIDAE		
Orchestia gammarella (Pallas)	Above H.W.M.	Similar
O. mediterranea A. Costa	Under stones, *Pelvetia* zone	Similar
Talorchestia deshayesii Audouin	In sand about H.W.M.	Similar
Hyale nilssoni (Rathke)	Under stones on mud	On *Enteromorpha* in rock pools (**8**); on weed (**3**)
AORIDAE		
Aora typica (Bate)	On *A. mentula*; on weed	Similar (**3**)
Lembos websteri Bate	On *Ascidia mentula*	On weed (**8**)
Coremapus versiculatus Norman	On *A. mentula*; on muddy shingle	6–22 m., Cette; 20–50 m., Ajaccio (**3**)
PHOTIDAE		
Microprotopus maculatus (Norman)	On weed on sand, lagoon	On sand, 0–24 m. (**3**)

Species	Oldany habitat	Other habitats
Isaeidae		
Isaea elmhirsti Patience	On lobsters	Similar everywhere
Amphithoidae		
Amphithoe rubicata (Montagu)	On mooring rope; on *Ascidia mentula*; between tide-marks	Between tide-marks; in dredgings (**8**)
Sunamphithoe pelagica (M. Edw.)	On *A. mentula*	On weed (**2**)
Corophiidae		
Corophium acherusicum (Costa)	♂♂ on *A. mentula*	Similar (**4**)
C. bonelli (M. Edw.)	On weed on sand, lagoon	Similar (**4**)
C. crassicorne (Bruzelius)	On weed on sand, lagoon	Similar (**4**)
Siphonectes dellavallei Stebbing	On weed on sand, lagoon	Clean sand (**8**); 2–20 m. (**3**)
Ericthonius braziliensis (Dana)	On *A. mentula*; on weed, lagoon	Similar (**3**)
Hyperiidae		
Hyperia galba (Montagu)	On jelly-fish	Similar everywhere

From the foregoing list little emerges that has not been mentioned by Goodhart and Harrison.

Certain species show a tendency to range upwards in this area from deeper water in the south. These are

Apelisca spinicarpa	Harpinia antennaria
Coremapus versiculatus	Siphonectes dellavallei

Other species also show a tendency to range into deeper water as they go still further southward. This is shown by *Ampelisca typica* whose vertical range lies between L.W.M. at Jersey to 77 m. off Corsica. *Coremapus versiculatus* goes down from L.W.M. at Oldany, through 6–22 m. at Cette, to 20–50 m. off Ajaccio. *Harpinia crenulata* follows the same trend from L.W.M. at Roscoff, through 10–30 m. at le Croisic to 20–40 m. off Ajaccio.

It is possible that this upward movement from south to north may be correlated with temperature. It is, perhaps, too easy to see more in this than there may really be. It is well known that many Amphipod species have a very wide range, extending from cold to tropic seas, regardless of temperature barriers. It is not necessary to mention more than a few of such widely distributed species to indicate how little temperature barriers seem to apply, e.g.

Lysianassa ceratina (A. Walker)	Britain to the Indian Ocean.
Aristias neglectus Hansen	Arctic Ocean to the Mediterranean.
Haploops tubicola Lillj.	Arctic Ocean to the Pacific Ocean.
Haustorius arenarius (Slabber)	Cattegat to Connecticut.
Urethoe elegans Bate	Norway to the Indian Ocean.
Amphilocus neapolitanus Della Valle	North Sea to Australia.

Of course it is not the same individuals which live at these extremes, and whether a specimen taken from a locality of high temperature and put into one of low temperature would survive is another matter.

A point of interest with regard to the species under discussion is the apparent discontinuity of their distribution. It is probable that these and other animals may roam about, tolerant of wide ranges of temperature, and

tend to settle where the temperature and/or other conditions are suitable. The suitability of the habitat would therefore be measured by the numbers of species therein. Thus the Oldany habitat is peculiar in that there is little or no wave action, a condition not generally typical of surface water. Also, since there is little water movement the temperature in the summer is rather higher than that of the outside water.

In general, the other species adhere fairly closely to their particular type of habitat. The great numbers of *Ascidia mentula* themselves almost form a particular habitat which seems to be attractive. With the exception of a few specimens scattered about, the bulk of the *A. mentula* population lives in the very still water of the basin. They are usually coated with a film of mud. But this mud can hardly be the particular attraction to the Amphipods because the stones etc. have a similar coating without the Amphipods. Why this habitat is so popular is not very clear unless it be that the Ascidians act as quite efficient water-circulators and consequently it would be to the advantage of other small animals to live within the influence of the water current.

It is not to be expected that highly specialized forms will vary their habitat. Thus *Bathyporeia guilliamsoniana*, *Urothoe elegans*, and *U. marina* are found in the sand, *Isaea elmhirsti* on lobsters and *Hyperia galba* on jelly-fish. The others are wanderers, capable of living permanently within a wide range of conditions.

What was rather unexpected was the complete absence (as far as investigation has shown), of certain species which occur in similar situations outside the harbour in the open sea. The salmon-net floats at Stoer yield an abundance of *Jassa falcata* (Montagu), yet anchor buoys in Oldany basin produced not one. *Gammarus stoerensis* Reid, which is fairly common on the open coasts, was not found in this area.

An attempt is being made to work out the general fauna of this interesting locality. A fairly large general collection has been made by Messrs Goodhart and Harrison. I have confined myself to the Amphipoda. This paper is based on material from their collection as well as my own. It is hoped that other papers will follow.

4. Summary

1. An attempt was made to work out the Amphipod fauna of a locality which is more northerly than those usually studied in Britain. It is also peculiar in that it consists of an almost land-locked shallow lagoon and a deeper basin, each with a different type of floor.

2. Besides the expected species collected, there occurred several which are normally associated with greater depth further south. This, taken in conjunction with other data, seems to indicate an upward ranging of species from south to north.

3. A few measurements were made to find if any differences existed between northern and southern forms of the same species (*Gammarus marinus*) in accordance with the Clines Theory. No significant differences were found.

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THE ECOLOGY OF THE AMPHIPODA IN A SMALL ESTUARY IN HAMPSHIRE

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(*With* 1 *Figure in the Text*)

CONTENTS

		PAGE
1.	Introduction	306
2.	Topography of the river	308
3.	Salinity of the water in the estuary	310
4.	Ecology of the estuarine species	
	Family Haustoriidae	311
	Family Gammaridae	311
	Family Talitridae	313
	Family Aoridae	314
	Family Photidae	315
	Family Corophiidae	315
6.	Species found outside the mouth of the estuary	317
7.	Discussion	318
8.	Summary	320
	References	321
	Appendix: list of species	322

1. Introduction

Several accounts of animals obtained from estuaries have previously been published. Most of these are general faunal lists for relatively large rivers. Even in these lists the Amphipoda have received scant attention; this is not perhaps surprising, for they are animals which can easily be overlooked, while the taxonomy of the two main estuarine genera is far from clear.

Gurney (1907) working on the fauna of some Norfolk estuaries touched briefly on the Amphipoda, but Crawford (1937 *b*) has shown that in the light of more recent work many of his names were incorrect. Poisson & Remy (1925) deal shortly with the Amphipoda of the Canal de Caen in France; while Schlienz (1923) and others have studied the Crustacea of the lower 120 km. of the Elbe. The most complete account of the distribution of estuarine Peracarida in England is that of Crawford (1937 *b*), who gives lists of Amphipoda from six estuaries in the west of England. These are based on one or two days' collecting each, with the exception of the river Tamar and its confluents, for which a rather more complete list is given. He also gives an extensive bibliography.

The present paper is the result of an investigation started in 1936 on the distribution of Amphipoda in the estuarine part of the river Afon Water in

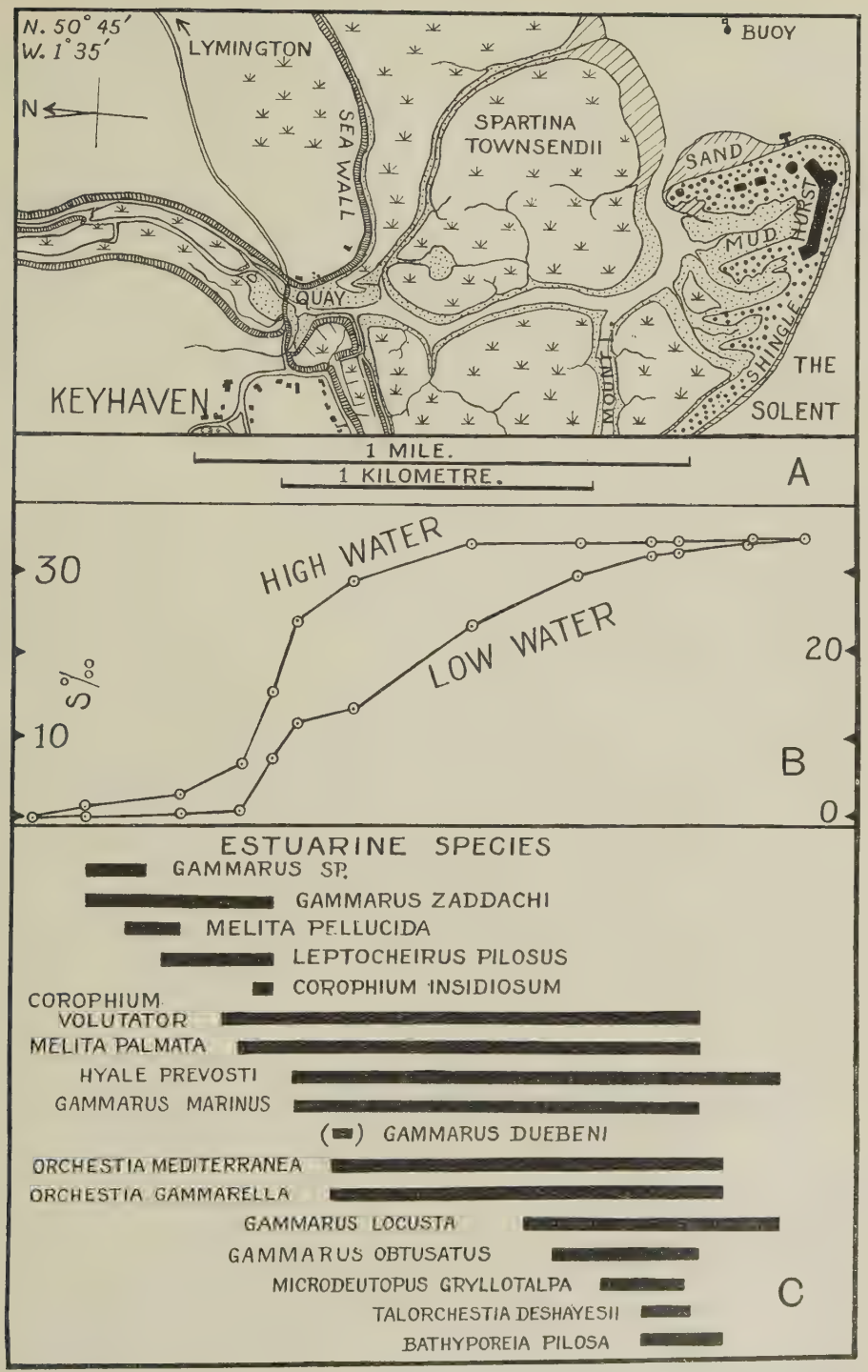

Fig. 1. A. Sketch map of the mouth of the river Afon Water, Hants. B. Graph showing the salinity at different points along the river. C. Estuarine species of Amphipod, showing their range in the river. .

Hampshire. The effect of the tide is felt only in the last mile and a half of the river, and so it has been possible to examine this relatively small area in far greater detail than was possible for the much larger estuaries on which the previous work has been done. Despite its small size, however, 18 different species of Amphipods were collected within the river itself. This is a larger number than has been recorded from any other single estuary, and only two brackish water species, *Gammarus chevreuxi* Sexton and *Corophium lacustre* Vanhöffen, were not obtained. These two are known to have a restricted range in England.

A further 25 species have been collected from the area immediately outside the mouth of the river, but these cannot be regarded as estuarine animals. A list of them is given at the end of this paper, and, so far as I know, it is the only list of marine Amphipods from this part of England.

2. Topography of the river

The river Afon Water is a small stream about 11 miles long rising in a lake 166 ft. above sea-level near Holmesley in the southern part of the New Forest. It flows down a wooded and often boggy valley winding its way between low heather-covered hills. Half a mile below Efford Mill, the point at which the river crosses the Lymington-Milford road, on its right bank there is a narrow strip of fresh-water *Juncus* marsh. In the winter this marsh is usually flooded, but the river itself is enclosed in a bank and is overhung by a thicket of hawthorn, blackthorn and similar trees growing on the banks.

About a mile and a half above the mouth of the river this embankment ends and the effect of the tide is felt here for the first time. There is a rise and fall of about a foot and at high tide the salinity is 0·6 $^{0}/_{00}$. At low tide it is completely fresh. The banks of the river below this are still steep but low, and the marshes on either side are flooded throughout the winter. In the 200 yd. above the end of the embankment the river bed rises a foot and no tidal movements are noticeable above this point. The river then flows for 400 yd. between banks covered by *Phragmites communis* and then broadens out into a sluice pond 3 acres in area. At low tide this pond dries out and the stream flows down a narrow channel between broad banks of very soft mud. At the lower end of the pond the river passes under a bridge through three sluice gates. When the tide is flowing, the gates shut and the water from the stream accumulates in the pond above them. During the flood a good deal of water leaks back into the pond through these gates.

There is a double tide in the river, as is usual in the estuaries of the Solent, and the second high tide is about an hour after the first. The result of this is that the river is full and the sluice gates are shut for about 2 hr. longer than they are open for each tide. During the second ebb the gates open and the water accumulated in the pond flows through them into a river which is here

much more marine in character. The estuary broadens out considerably, and on each side there are broad flats of rather gravelly mud exposed at low tide. The flats are enclosed on all sides but the south, by stone dykes. Most of the land behind these walls is below the level of the water at high tide, and is extensively flooded when the sea walls break, as sometimes happens. On the right bank of the river there is a derelict wooden quay in front of the stone sea wall, and behind the wall is a low-lying marsh of *Spartina townsendii* and *Glyceria maritima*, traversed by ditches which drain into the river through small sluices. Below this quay the river flows down towards the sea between the mud flats covered by *Spartina townsendii* so characteristic of the Solent. At high tide the roots of the grass are covered by a few inches of water. The Spartinetum ends in a 'salting cliff' about a foot high formed by mud matted together by the roots and rhizomes of the grass. The Isopod *Paragnathia formica* (Hesse) is common in burrows on the face of this cliff.

About half a mile west of the river the *Spartina* flats are bounded by a shingle bank, running out as a spit from the land. It ends as the peninsula of Hurst at the mouth of the river Afon Water. This is a broad flat expanse of shingle, now colonized by *Inula crithmoides*, *Limonium vulgare*, *Obione portulacoides*, *Glaucium luteum* and various other halophytes, and on its higher points by various grasses and brambles. There are no sand dunes. On the Point is an obsolete fort, a lighthouse and several cottages. The spit ends in a long terminal point running north at an acute angle to the shingle bank, while before this there are three shorter lateral points. The spit is an old one, its present terminal point having been in existence for at least four centuries, and it is unlikely ever to extend farther, as does the much more recent one at Blakeney in Norfolk. The terminal point, however, is still growing slowly northwards. The shingle bank connecting Hurst to the mainland is moving east at a rate of several feet a year, and when the lateral ridges were formed they would not have made the unusually acute angle to the bank that they do now. The origin and vegetation of Hurst Point and of the similar one at Blakeney are fully discussed by Oliver (1912).

Between the lateral points there are three broad but shallow creeks joining the main river just above its mouth. They are bounded by shingle beaches running down from the lateral ridges, and below high water of neap tides there is a zone of *Fucus* sp. attached to the pebbles of the beach. These arms of the river dry out almost completely at low tide and leave flats of very soft and deep grey mud which cannot be crossed on foot without mud-pattens. Lying on the mud there are often extensive mats of a filamentous green alga. The area of mud covered by this alga varies from year to year, but in 1939 it was small. In the southern end of the centre creek is a large bed of *Zostera nana* growing on the mud. Outside the mouth of the river, round the terminal point of Hurst, there are broad flats of sand exposed at low-water spring tides. On the southern side of the channel the sand is fairly clean and runs up to the

edge of the shingle, meeting it just above L.W.N.T., while to the north of the river it is stony and rather muddy, especially at its upper part, where it meets the edge of the Spartinetum. Six years ago these flats were covered by *Zostera marina*, but this plant is now almost extinct. Considerable areas of the flats are, however, still covered by masses of mud held together by its dead rhizomes.

3. Salinity of the water in the estuary

A series of water samples were taken on 30 June 1939. There had been a slight shower the day before, but no rain for the preceding week, and the amount of fresh water coming down the river can thus be regarded as about the average for the time of year. Full moon was at 16.16 hr. on 1 July, and so the tide was just beginning to get into springs; low water was about 9 in. above that during full springs.

The samples were taken from a boat as quickly as possible during slack water at both high and low tide. Each series was completed in about half an hour. They were titrated with silver nitrate, and the total weight of salts per litre calculated according to the formula given by Harvey (1928). The results are shown graphically in Fig. 1 A.

The salinity in mid-Solent was just under 34 $^0/_{00}$ and did not vary noticeably with the state of tide. At low tide even just inside the mouth of the estuary the salinity was 32·6 $^0/_{00}$, and the water became more dilute farther up the river. The salinity of the fresh water from the stream is increased farther down the estuary as it becomes mixed with the salt water draining off the mud and *Spartina* flats. At the mouth of the river the channel is deep (there is 19 ft. just above the bar at L.W.M.S.), and so even at low tide there is a considerable reserve of salt water here. In the sluice pond the salinity of the water at low tide is 7·2 $^0/_{00}$ just above the gates. This is due to the more saline water draining out from the flats exposed at low tide into the fresh-water stream flowing in a narrow channel in the middle of the mud. A few hundred yards above the sluice pond where there are no mud-flats the water is fresh, its salinity being only 0·6 $^0/_{00}$ at low tide. During springs the tidal rise is 8 ft. and 6 ft. in the neaps at Hurst, and therefore when the tide turns a considerable body of water from the Solent enters the estuary and the current in the river is reversed. The more dilute water, which at low tide had got down to the mouth, is pushed back up the river again, and the salinity of the water in the creeks at Hurst and half-way up to the quay is 33·5 $^0/_{00}$ or more, and is thus almost undiluted Solent water. The fresher water which has been pushed up the river accumulates in the channel and over the mud-flats opposite the quay at Keyhaven. Here even at high tide the salinity is below 30 $^0/_{00}$, while just below the sluice gate it is 24·0 $^0/_{00}$. The water in the sluice pond is usually 3 or 4 ft. below the level of that on the other side of the gates, and some of the more salt water leaks through the gates into the pond and raises its salinity.

At high tide this is 15·8 $^0/_{00}$ near the sluice; a high figure, when it is remembered that the salt can only get in through the leaky gates and that most of it is removed again during the ebb. In the middle of the pond, however, it is reduced to 6·0 $^0/_{00}$. At low tide when the gates are open there is little difference between the salinity of the water above them and in the quay below. The effect of the salt water leaking through the sluice gates is not felt far above the pond; 150 yd. above it in the Phragmitetum, even at high tide, the salinity is only 3·0 $^0/_{00}$. The salinity of the river must vary considerably, and during the winter or after heavy rain the figures would be much lower.

4. Ecology of the estuarine species

Family **Haustoriidae**

Bathyporeia pilosa Lindström is the only species of this genus to occur inside the mouth of the estuary. It is found on a gently sloping bank of muddy and rather pebbly sand just round the point of Hurst Spit. It ranges from between a point rather below H.W. neaps down to L.W.M. of neap tides. *B. pilosa* is the only member of the genus which can endure any dilution of the water, and in some cases it is said to extend some way up estuaries. At Keyhaven, however, there is no sand suitable for it further up the river. The species is also found occasionally just outside the mouth of the river.

Two more species of *Bathyporeia* occur just outside the mouth of the river: *B. guilliamsoniana* (Bate) on the banks of clean sand uncovered at L.W.M.S. to the south of the channel, and *B. robertsoni* Bate on the rather muddier banks to the north of it. *Urothoë brevicornis* Bate occurs on the south banks of clean sand, occupying a zone below that of *Bathyporeia guilliamsoniana*, just below L.W.M. of ordinary springs.

Family **Gammaridae**

Melita pellucida G. O. Sars, is rather rare but a few specimens can usually be found in the ditches which drain into the main river from the marshes above the sluice gates. The salinity of the water here is very low and contains only 2 or 3 $^0/_{00}$ even at high tide. At low tide it is fresh. The species is an inconspicuous one which is easily overlooked, and at Keyhaven it has only been found among the roots of grasses and reeds which have been uprooted and are lying in the ditches.

Melita palmata (Montagu) is one of the commonest and most widely distributed of the Amphipods in the estuary. It is nearly always present under any stone or piece of wood lying on mud or on the muddy gravel opposite the quay and at the mouth of the river. Small specimens are usually found in the masses of filamentous green algae lying on the mud flats or in the pools at the edge of the Spartinetum. These small specimens are easily mistaken in the field for *M. pellucida*. The species extends from the mouth of the river right up into the sluice pond where, however, it is not common.

Gammarus pulex (L.) has not been found in the Afon Water, but it was not possible too look for it very thoroughly. According to Reid (1939*a*) *G. pulex* does not seem to occur in acid streams in Ireland where it is replaced by *G. duebeni* Lilljeborg, var. α Reid. The upper part of the river was examined but neither of these species was found. *G. pulex* may very well be present lower down, but no search was made below the boundary of the New Forest. Serventy (1935) states that in the river Deben in Suffolk *G. pulex* occurs in the non-tidal part of the estuary and gives way to *G. zaddachi* in the brackish part, which in turn is replaced by *G. locusta* at the mouth of the river.

Gammarus zaddachi Sexton is the commonest species of Amphipod in the upper reaches of the estuary above the sluice gates. The maximum salinity in which it was found was 15·8 $^0/_{00}$, and it extends up to the upper limit of the tidal area. In the lower part of its range it is abundant in and around the tufts of *Fucus* sp. which lie on the bottom of the sluice pond, while higher up the river rather smaller specimens are common in the grasses and rushes which trail in the water from the river bank.

Gammarus duebeni Lilljeborg var. β Reid, the other common British brackish water Gammarid, is very local and rare at Keyhaven and is not found in the river itself. A few years ago it was abundant among weeds in a small ditch in the marsh inside the sea wall on the west bank of the river below the quay; but since this ditch was cleaned and a new and more efficient sluice installed at the end of it the species has become almost extinct. In June 1939, six specimens were collected after a careful search. The salinity of the water in the ditch at this time was 7·7 $^0/_{00}$ at high and 5·1 $^0/_{00}$ at low tide, but with the old sluice, which was very defective, it was probably a good deal higher than this. Apart from a few *Leptocheirus pilosus*, no other Amphipods have been found associated with *Gammarus duebeni*.

Gammarus chevreuxi Sexton is another species of this genus which is known to occur in brackish waters in the British Isles. Pentelow (1931) records it from inland brackish water near Coventry, but apart from this it is only found in the estuaries of Devon and Cornwall. Crawford states that it did not occur in various rivers which he had examined on the south and east coasts of England. Its absence from the river Afon Water is therefore what would be expected.

Gammarus marinus Leach.[1] This species lives amongst the Fucoids which grow on stone walls and wooden piles or booms in the river. It extends up as far as the quay into water with a maximum salinity of 24·0 $^0/_{00}$, but above the sluice gates it is replaced by *G. zaddachi*. Farther down the river it is found in the Fucoids growing on the pebbles of the beaches bordering the three broad creeks at Hurst and also on the stone-work of the small quay at Hurst Castle.

[1] There is a difference of opinion as to whether this and the following species should be placed in the genus *Gammarus* or in the new genus *Marinogammarus*. It was decided for the moment to use the old genus. The species here referred to is *G. marinus, sensu stricto*. Editor.

Here, however, *G. marinus* occurs only in the zone between a line somewhat below high water and somewhat above L.W.M. of neap tides. Any Fucoids growing on stones, or lying on the flats below this zone, are usually occupied by *G. obtusatus* Dahl or *G. locusta* (L.). The latter is seldom found above L.W.N.T., but *G. obtusatus* often extends up into the *G. marinus* zone, though the two species never occur together. It is possible that these species are confined normally to different species of algae. Neither is found outside the mouth of the river.

Gammarus olivii M.-Edw. This species lives under deadleaves lying on the bottom of the river near the upper limit of the tidal areain water whose salinity is less than 1 $^0/_{00}$ at high tide, and which is entirely fresh when the tide is out. Morphologically it resembles in some ways *G. stoerensis* Reid, which according to Stephensen (1938) is entirely marine.

Gammarus obtusatus Dahl. This species has only been noticed in the British Isles in the last few years; but it appears to be quite common and widely distributed, and to have been confused with *G. marinus*, to which it bears a very close resemblance (Reid, 1939 *b*). In the estuary at Keyhaven it does not extend far up the river, but occurs in Fucoids growing on stones and stumps on the mud-flats opposite Hurst and also on the pebble beaches bordering these flats to the south. As has been noted above, *G. obtusatus* usually occupies a zone below that of *G. marinus*, between L.W. of neaps and springs, although it is occasionally found higher up. It does not occur outside the mouth of the river.

Gammarus locusta (L.) is the only species of *Gammarus* found outside the mouth of the river at Keyhaven, where it is very common. Inside the estuary it occurs rather sporadically in the lower reaches, but has only once been found above the junction of Mount Lake with the main river. The species is always found near L.W.M.S. and exists in two varieties, a rather large brown and strongly sclerotized form found amongst the red and brown algae which grow on stones lying on the mud flats, and a smaller pale green fragile variety living in the mats of filamentous green algae which lie on the mud in some places. These differences are probably environmental and without any genotypic significance, but it is hoped that a more complete investigation of this question may be made at some future date.

Family **Talitridae**

Hyale prevosti (Milne-Edw.) (=*H. nilssoni* Rathke) extends up the river as far as the quay into water whose salinity at high tide is 24·0 $^0/_{00}$. It does not occur above the sluice gates. In the upper part of the river it is present only in the tufts of *Fucus vesiculosus* L. and *Ascophyllum nodosum* Le Jol. growing on the stone walls and wooden piles round the old quay and is almost invariably found together with *Gammarus marinus*. The individuals vary in colour from light brown to black. Farther down the river it is found among the Fucoids

with *G. marinus* and also in the lower zone occupied by *Gammarus obtusatus*. Besides this, however, rather smaller light green specimens occur in the mats of green algae lying on the mud flats. They are hard to see in this situation and rather scarce, but a small number is always present. A few large deep emerald green specimens can usually be taken from amongst the algae on the buoys right out in the Solent. As far as can be seen these varieties differ only in their size and coloration, but each seems to be confined to its specific habitat.

Talorchestia deshayesii (Audouin) was found only on a very small sandy beach at the mouth of the river, just round the point of Hurst Spit. It is abundant here, living in burrows in the dry sand between high-water neaps and the highest point reached by spring tides. The beach on which it lives is only about 25 yd. in length.

Talitrus saltator (Montagu) is the commonest of the British 'sandhoppers', but was not found at Keyhaven. It usually lives round H.W.M.S. in jetsam lying on sand, and so the only suitable habitat for it would be with *Talorchestia deshayesii* on the small beach described above. No reason can as yet be suggested for its absence from this locality.

Orchestia. The taxonomy of this genus is very confused, and a thorough revision of it would be desirable. The distribution of the different species was therefore difficult to determine, and it is hoped that a more detailed account may be given in a further paper.

Orchestia gammarella (Pallas) is found at Hurst in the line of dead *Spartina* and other jetsam cast up at H.W.M.S. On the quay it occurs mainly amongst the salt marsh vegetation inside the sea wall where, however, it is not common.

Orchestia mediterranea A. Costa is represented by fairly typical specimens in the jetsam at H.W.M.S. on the river bank opposite the quay at Keyhaven.

At least one other apparently undescribed species or subspecies related to *O. mediterranea* was found in burrows or cracks in the earth under *Obione portulacoides* and other saltmarsh plants growing above high-water mark of normal spring tides on Hurst Spit. Besides these, several atypical members of the above species were found, and it is not at present clear whether these should be regarded as further separate subspecies.

Family **Aoridae**

Microdeutopus gryllotalpa A. Costa is rather rare at Keyhaven, but a few specimens can always be obtained from the bed of *Zostera nana* in the middle of the three creeks by Hurst Castle, and it has also been taken from pools just below the edge of the *Spartina* cliff on the north bank of the river opposite Hurst. It does not occur outside the mouth of the river, but it cannot be regarded as a true brackish water animal since the salinity exceeds 33·5 $^{0}/_{00}$ at all states of the tide in both its habitats. The reason for its absence outside

the river is probably that it can live only over a muddy bottom. Crawford (1937*b*) records the species from some way up the river Lynher 2 miles from Plymouth Sound, but according to Percival (1929) the salinity here is 32·6 $^0/_{00}$, so that it could scarcely be described as brackish.

Family **Photidàe**

Leptocheirus pilosus Zaddach is a widely distributed estuarine Amphipod characteristic of the less saline waters. At Keyhaven it is not found in the river below the sluice gates, but is common in the sluice pond, and extends for several hundred yards up the river through the *Phragmites* marsh. At its highest point the salinity at high tide is only 3·0 $^0/_{00}$. This animal lives in tubes of mud built against the flat surfaces of stones, or on the thallus of *Chondrus crispus* Lyngb. It is sometimes found in rather less well-defined tubes built amongst the tufts of filamentous red algae inhabited by *Corophium insidiosum* Crawford. The bionomics of this species were dealt with more fully in a previous paper (Goodhart, 1939).

Family **Corophiidae**

Corophium volutator (Pallas) is the most abundant species of the family in the estuary. Characteristically it lives in semi-permanent burrows built in the upper 4 in. of soft grey mud on the flats. It is, however, found also in muddy sand.

This animal is very common on the broad mud-flats at the mouth of the river and in the three creeks by Hurst. It ranges from L.W.M.S. right up to the edge of the '*Spartina* cliff' and is found on all the mud excepting that which is covered by the mats of filamentous green algae. It does not occur, however, on the steep banks of the runnels and ditches which drain the flats at low tide. The density of the species was estimated at about 300 per sq. m., not including animals too small to be retained by a 2 mm. sieve. Farther up the estuary, *C. volutator* is found in the small pools at the edge of the Spartinetum. In some places the grass is dead or moribund for several yards from the edge of the 'salting cliff' formed by mud bound together by its rhizomes. The edge of this cliff is undermined and eventually collapses, but before this happens small pools are left in the depressions amongst the dead *Spartina* which are filled only at high tide, and which never drain out completely. *C. volutator* is usually present in these pools, but the specimens are seldom so large as those found on the mud-flats. It was never found on the mud around the stems of the healthy plants in the middle of the Spartinetum. In this part of the estuary the animal was not found on the comparatively steep mud-banks of the river below the edge of the *Spartina* cliff; but it is usually present where a flat spit of mud projects out from these banks, e.g. on the convex corner of a bend in the river. Still higher up the estuary, small specimens occur on the mud-flats opposite

the quay at Keyhaven. The mud here is rather gravelly, and in parts almost sandy, and it is usually possible to walk over it without mud-pattens. Above the sluice gates the species is again abundant in the mud at the bottom of the pond, and some of the largest specimens obtained from the whole estuary were found here. The mud in this pond is very deep and soft, but differs from that below the sluice in containing a lot of undecomposed vegetable matter. The species is not found any farther up the river, since it narrows down and there are no suitable mud-flats for it.

It is thus seen that *C. volutator* has a greater range of salinity than any other of the Amphipods found, with the exception of *Melita palmata* which, however, is rare above the sluice gates. It extends from the mouth of the estuary, where at most stages of the tide the river is filled with Solent water, right up to the middle of the sluice pond, where the salinity was 6·0 $^{0}/_{00}$ at high tide. After heavy rain the water here can scarcely be brackish at all.

C. volutator is usually regarded as being confined to flats of the softest and finest mud (Hart, 1930). At Keyhaven, however, besides being found on this type of mud the animal also occurred in sand. It was common in the sand at the bottom of some small pools on Hurst Spit which are filled only at the highest tides but which do not drain dry. It was also fairly common in a patch of rather muddy and gravelly sand just inside the point of the spit. Here it occurred with *Bathyporeia pilosa*, and when the sand was sieved the two species were obtained in the same sieveful. This is unusual, and I know of no other recorded occurrence of *Corophium volutator* from anything but the finest mud, while *Bathyporeia pilosa*, like all the other Haustoriids, is essentially a burrower in sand.

Corophium arenarium Crawford, a species very closely related to *C. volutator* is found burrowing in sand, and might have been expected to have occurred at the mouth of this estuary. The specimens obtained from sand at Hurst were, however, submitted to Mr Crawford who stated that they were identical with *C. volutator*. Further investigation of these closely allied species may show that *C. arenarium* is in fact only a variety of *C. volutator*, as was suggested by Crawford (1937*a*) in his original description of the species.

C. volutator lives only on the very flattest banks either of mud or sand, and it is not found on the steep sides of the runnels which drain them nor on the mud-banks of the river where they are narrow and steep. Hart has suggested that this was due to the fact that really flat mud-banks do not drain off completely at low tide, but are always covered with shallow pools of water in which the animals can lie without danger of exposure to the air. This is certainly the case for the lower part of the flats, but *C. volutator* extends right up to the edge of the Spartinetum, from which the water drains off fairly completely. Furthermore, at low tide some specimens can always be seen crawling about over the mud and out of the shallow pools on it. On the sand-bank at the mouth of the river where the species is found the water drains off

completely from the sand, though here the animal does not crawl about over the surface at low tide.

A more likely reason for the absence of the species from the steeper banks is that the animals would get washed off the banks by the current, which flows rapidly in the main channel of the river, both on the flood and particularly on the ebb-tide. Although *C. volutator* is a burrowing species, it spends quite a lot of its time out of its burrow; and in the shallow water just before the flats dry off many specimens can be seen swimming or crawling over the mud. On the banks of the main channel these would be swept away in the stream; but over the broad and shallow flats away from it, there is never a strong current, and it is only here that a comparatively weak swimming animal can live.

Corophium insidiosum Crawford is confined in England to brackish water. According to Dahl (1938), however, it is found outside the estuaries in the Baltic. It is probably fairly common in the rivers of Great Britain although there are few records. At Keyhaven it occurs only in the sluice pond, and builds tubes of mud and algal fragments among the dense tufts of various filamentous red and green algae which grow on stones and especially on the brickwork leading up to the sluice gates. The animal is very abundant in the silt on the bottom of a long drain leading from the western corner of the pond under the road, and through a small sluice into the quay. Very little light reaches the end of this drain. The species is not found below the sluice gates nor in the river above the pond.

Corophium lacustre Vanhöffen. Despite a careful search this animal was not found in the Afon Water: according to Crawford it appears to be confined in England to the estuaries of Norfolk, where it is found in brackish water instead of *C. insidiosum*.

6. Species found outside the mouth of the estuary

The following truly marine species were found outside the mouth of the river, all in the area shown on the map in Fig. 1A. It has been possible to give only the briefest notes of the different types of environment inhabited by the different species, but it is believed that this is the only published list of marine Amphipods from this part of the country. The different types of environment are divided up as follows:

(1) Burrowing in the muddy sand on the banks uncovered to the north of the channel at L.W.M.S.

Bathyporeia robertsoni Bate — Ampelisca brevicornis (A. Costa)

(2) Under stones and in algae lying on these banks:

Calliopius laeviusculus (Krøyer) — Gammarellus angulosus (H. Rathke)

Cheirocratus sundevalli (H. Rathke) — Gammarus locusta (L.)

Dexamine spinosa (Montagu)

(3) Burrowing in the cleaner sandbanks exposed at L.W.S.T. to the south of the channel:

Bathyporeia guilliamsoniana (Bate) — Urothoë brevicornis (Bate)

(4) In the beds of *Zostera marina* at and just below L.W.M.S. on both sides of the channel. The Zostera is now almost extinct:

Aora typica Krøyer
Dexamine spinosa (Montagu)
Ericthonius brasiliensis (Dana)
Gammarus locusta (L.)
Microprotopus maculatus Norman
Nototropis swammerdam (Milne-Edw.)

(5) Among algae and sponges growing on the old wooden pier opposite Hurst Castle:

Calliopius crenulatus Chev. & Fage
Corophium crassicorne Bruzelius
Jassa falcata (Montagu)
Melita gladiosa Bate
Nototropis falcatus (Metzger)

(6) Boring into the wooden piles of the pier:

Chelura terebrans Philippi

(7) Among the holdfasts of *Laminaria* sp. growing round the pier at L.W.M.S.:

Aora typica Krøyer
Eurystheus maculatus (Johnston)
Jassa dentex (Czerniavski)
Lysianassa ceratina (A. Walker)

(8) In dead crabs on the sand:

Orchomenella nana (Krøyer)

(9) Among the mouth parts of the crab *Maia squinado* trawled off Hurst:

Isaea montagui Milne-Edw.

(10) Among algae on the Royal Lymington Yacht Club's Racing Buoy, off Hurst:

Calliopius crenulatus Chev. & Fage
Corophium acherusicum Costa
Dexamine spinosa (Montagu)
Gammarellus angulosus (H. Rathke)
Gammarus locusta (L.)
Hyale prevosti (Milne-Edw.)
Jassa falcata (Montagu)

(11) Commensal with large Medusae:

Hyperia galba (Montagu)

7. Discussion

It is important to remember, when assessing the limits of salinity which can normally be endured by a species, that in many cases the animals are not covered by water at low tide, and so they could live in a part of the river in which the salinity at low water is below the minimum in which they can survive. In the following notes therefore the salinity at high tide is given for the limits of their distribution, since the volume of water entering the estuary on the flood in such a shallow river is greatly in excess of that in the river at low tide. The salinity therefore should reach a figure near to its high-tide value comparatively soon after the flood has set in, and should retain it on the ebb until most of the water is out of the river. In the winter or after heavy rain the high-tide salinity will of course be decreased; but for the lower part of the river the effect of this reduction will probably be less than might have been supposed. Even when the river is in flood, the volume of water getting through the sluice gates on the ebb during the four hours or so that they are open must be much less than that of the Solent water which fills the estuary on the flood tide. Above the sluice gates, however, the effect of rain will be much greater since very little of the salt water can get through them into the river above.

The animals found in an estuary can be divided into four groups according to their toleration of different water salinities.

(1) Species which are wholly fresh water, and can endure no salt at all, e.g.:

Gammarus pulex — G. duebeni var. α

both of which however probably do not occur in this particular estuary.

(2) Truly brackish species which can live permanently in neither entirely fresh nor entirely salt water, e.g.:

Gammarus zaddachi (0·6–15·8 ‰)	Leptocheirus pilosus (15·8–3·0 ‰)
Gammarus olivii (0·6 ‰)	Gammarus duebeni var. β (7·7 ‰)
Melita pellucida (0·6–3·0 ‰)	Corophium insidiosum (15·8 ‰)

(3) Marine species which are, however, tolerant of a certain dilution and extend some distance up the estuary. The degree of tolerance exhibited by the species varies, and so different species range for different distances up the river, e.g.:

Corophium volutator (6·0 ‰)	Gammarus obtusatus (33·5 ‰)
Melita palmata (13·0 ‰)	G. locusta (33·5 ‰)
Gammarus marinus (24·0 ‰)	Microdeutopus gryllotalpa (33·5 ‰)
Hyale prevosti (24·0 ‰)	Bathyporeia pilosa (33·7 ‰)

The figures in brackets after the name is the minimum salinity at high tide in which the species is found.

(4) Truly marine species found around the mouth of the estuary, where the sea water is not noticeably diluted by fresh water from the river.

Although the most obvious and probably the most important factor affecting the distribution of animals in an estuary is the salinity, there may be other considerations of equal significance. The type of bottom and supply of suitable food are of great importance, though both of these may to a certain extent be affected by the salinity.

Often, however, salinity is the limiting factor. This is well shown when the Amphipods found above and below the sluice gates are considered. There is a salinity difference of 10 ‰ between the high-tide values on either side of the gates and only two species, *Melita palmata* and *Corophium volutator*, were found on both sides despite the fact that, apart from the salinity, conditions were very similar on each side. There were Fucoids in the sluice pond very similar to those below it, and yet both *Gammarus marinus* and *Hyale prevosti* were entirely absent from them, while *Gammarus zaddachi*, though abundant in the pond, did not occur below it. Similarly, *Leptocheirus pilosus*, which builds tubes on the fronds of *Chondrus crispus* in the sluice pond, was entirely absent from the lower parts of the river, despite the fact that *Chondrus crispus* extends down to the mouth. In the same way *Gammarus locusta* is found in the mats of filamentous green algae lying on the mud-flats at the mouth of the river, and yet is absent from the very similar algae on the flats opposite the quay. From these examples it seems that salinity is really the factor which limits the distribution of these species.

On the other hand, *Bathyporeia pilosa*, which is said to be able to withstand a certain dilution of sea water, is, nevertheless, confined to the extreme mouth of the estuary at Keyhaven, where conditions are almost marine. It could probably extend for some distance farther up the river, were there any suitable sandy flats for it. For the same reasons it is difficult to decide how far

up the estuary *Corophium volutator* could penetrate. There is an extremely vigorous colony in the mud on the bottom of the sluice pond in water which had a salinity of 6·0 $^0/_{00}$ at high tide, but which must be almost fresh for long periods in wet weather. There are no suitable mud-flats for it above the sluice pond, but if there were it might well reach right up to the limit of tidal action, or indeed farther.

It is not known what it is that limits the distribution of *Gammarus duebeni*, but it cannot be salinity, for the species is found in a ditch where the salinity was 7·7 $^0/_{00}$—which is well within the range of *G. zaddachi* (0·6–15·8 $^0/_{00}$), though the two species were never found together. It may be that the explanation of this is to be found in the *p*H of the water, though this was not measured at Keyhaven. According to Palmer (1933) *G. zaddachi* and *G. duebeni* are found together in the same ditch at Tollesbury in Essex, where perhaps the *p*H may be within the range of both species.

Several species, e.g. *G. marinus*, *G. obtusatus*, *Corophium volutator* and *Melita palmata*, are found in the estuary and some way up it but, although extending down to the mouth, are not found beyond it out in the Solent. It should not, however, be assumed that they are limited to the estuary by their inability to survive the full salinity of Solent water. Indeed, the salinity inside the mouth of the river opposite Hurst Castle is not significantly different from that in the Solent during the greater part of the day when the river is full, and so it may perhaps be assumed that a species which reaches down to the mouth of the river could, as far as salinity is concerned, extend beyond it. Some species, *Hyale prevosti* and *Gammarus locusta*, do occur in the Solent but others do not. Since, apart from salinity, conditions just outside the mouth are very different from those in the river, this is perhaps not surprising. In the estuary, *Corophium volutator* and *Melita palmata* are both found on mud, and are unable to live on the flats of comparatively clean sand outside the mouth, where there are no growths of Fucoids suitable for *Gammarus marinus* or *G. obtusatus*. That these two species are not limited to the estuary by salinity is shown by the fact that both are common among the Fucoids growing on rocky shores in other parts of Great Britain. *Corophium volutator* is seldom found excepting in an estuary, but this is due more to the need of a muddy habitat rather than to a brackish water one, and mud is comparatively rare on an open shore.

8. Summary

1. The topography of a small estuary in Hampshire, the Afon Water, and the penetration of salt water into its estuarine part are described.

2. An account is given of the ecology and distribution of the 18 species of Amphipoda found in the river itself, together with figures for the limits of salinity in which these species are found, while the other factors affecting their distribution are also discussed.

3. One of the species, an *Orchestia*, is probably new to science, but no description of it is published in the present paper.

4. A list of 25 more marine species of Amphipoda from outside the mouth of the river in the Solent is also given.

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APPENDIX: LIST OF SPECIES

I. *Estuarine species*

Fam. Haustoriidae
- Bathyporeia pilosa Lindström

Fam. Gammaridae
- Melita pellucida G. O. Sars
- Melita palmata (Montagu)
- Gammarus zaddachi Sexton
- Gammarus olivii
- Gammarus duebeni Lilljeborg var. β Reid
- Gammarus marinus Leach
- Gammarus obtusatus Dahl
- * Gammarus locusta (L.)

Fam. Talitridae
- * Hyale prevosti (Milne-Edw.)
- Talorchestia deshayesii (Audouin)
- Orchestia gammarella (Pallas)
- Orchestia mediterranea A. Costa
- Orchestia sp.

Fam. Aoridae
- Microdeutopus gryllotalpa A. Costa

Fam. Photidae
- Leptocheirus pilosus Zaddach

Fam. Corophiidae
- Corophium volutator (Pallas)
- Corophium insidiosum Crawford

* Species also found outside the mouth of the estuary.

II. *Wholly marine species*

Fam. Lysianassidae
- Lysianassa ceratina (A. Walker)
- Orchomenella nana (Krøyer)

Fam. Ampeliscidae
- Ampelisca brevicornis (A. Costa)

Fam. Haustoriidae
- Bathyporeia guilliamsoniana (Bate)
- Bathyporeia robertsoni Bate
- Urothöe brevicornis Bate

Fam. Calliopidae
- Calliopius laeviusculus (Krøyer)
- Calliopius crenulatus Chev. & Fage

Fam. Atylidae
- Nototropis swammerdami (Milne-Edw.)
- Nototropis falcatus (Metzger)

Fam. Gammaridae
- Gammarellus angulosus (H. Rathke)
- Cheirocratus sundevalli (H. Rathke)
- Melita gladiosa Bate

Fam. Dexaminidae
- Dexamine spinosa (Montagu)

Fam. Aoridae
- Aora typica Krøyer

Fam. Photidae
- Microprotopus maculatus Norman
- Eurystheus maculatus (Johnston)

Fam. Isaeidae
- Isaea montagui Milne-Edw.

Fam. Jassidae
- Jassa falcata (Montagu)
- Jassa dentex (Czerniavski)

Fam. Corophiidae
- Ericthonius brasiliensis (Dana)
- Corophium crassicorne Bruzelius
- Corophium acherusicum Costa

Fam. Cheluridae
- Chelura terebrans Philippi

Fam. Hyperiidae
- Hyperia galba (Montagu)

THE TEMPERATURE PREFERENDUM OF CERTAIN INSECTS[1]

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(*With Plate 9 and 10 Figures in the Text*)

CONTENTS

		PAGE
1.	Introduction	323
2.	Previous literature	324
3.	Description of temperature gradient apparatus	330
	(*a*) Williams's early apparatus	330
	(*b*) Brass trough with ice-box	330
	(*c*) Brass trough with Thermos vacuum flask	332
4.	Technique of experiments	332
	(*a*) Apparatus and working precautions	332
	(*b*) Observations	335
	(*c*) Insects used	337
5.	Results	341
	(*a*) Stored product insects	341
	(*b*) Soil insects	348
	(*c*) Other insects	349
6.	Discussion	351
7.	Summary	354
	References	355

1. Introduction

Although much work had been done on the optimum temperature for various insects, and the maximum and minimum temperature necessary to maintain life, relatively little has been done on their preferred temperature. In fact, at the time the present work was started only one worker in England had ever published on this subject.

In order to avoid any possible confusion between optimum and preferred temperatures it might be well to define them before going further. Although it is realized there are many definitions of the optimum temperature of an insect, for the purpose of this work it is taken to mean the temperature at which the greatest number of insects are reproduced in a given period of time. In other words, it is the temperature at which the relation between the number of eggs laid, the length of life and the mortality is such that the largest numbers of individuals survive after a given time. The temperature preferendum, on the other hand, is the temperature to which an insect moves if given its choice of a temperature gradient.

[1] Part of a Thesis presented to the University of London for the Degree of Ph.D.

The term 'preferendum' was proposed by Dr C. B. Williams while in Egypt, in 1922, although he never published on this subject himself. Since then various workers have adopted the term in one form or another. Herter has used 'thermische Indifferenzzone' and 'thermotaktisches Optimum'. Bodenheimer & Schenkin used 'Vorzugstemperatur'. More recently Gunn has suggested the term 'eccritic' temperature.

Temperature preferendum work may be approached from three different angles. (*a*) A comparative study of the temperature reactions of a large number of representative insects from various orders. (*b*) A comparative study of such factors influencing the temperature reactions as: age (larvae and adults), sex, insects tested with and without food, insects previously kept at room and at a constant high temperature, and the environment or natural habitat of the insect (those inhabiting soil, water, stored products, and also parasitic insects, etc.). (*c*) A detailed physiological study of one species to determine why it prefers a certain temperature or why it reacts as it does. Obviously this latter work could not be undertaken until (*a*) and (*b*) had been at least partially investigated. Because of a time limit, as much of the present work as possible was done under the first two groups.

The writer wishes to thank in particular Dr C. B. Williams for suggesting this problem and for his always unfailing help and advice; also the other members of the Entomology Department of Rothamsted Experimental Station for the helpful atmosphere found there.

2. Previous literature

As stated above, the first to carry out work on the temperature preference of insects was Williams in 1922 in Egypt. However, this early work was never published and the only reference to it is Kirkpatrick (1923) in his work on the Egyptian cotton-seed bug (*Oxycarenus hyalinipennis*). Kirkpatrick states: 'The resting bugs were found, by means of an apparatus devised by Mr C. B. Williams, to be thermotropic to a temperature of 36° C.'

Herter (1923 *a* and *b*, 1924, 1925) carried out some preferendum studies on insects. His apparatus ('Temperaturorgel') consisted of a cage 61 cm. long, 10 cm. high and 3 cm. wide, with an aluminium floor, a cardboard roof and glass sides. The metal floor was heated at one end with a gas flame and the heat lost to the opposite end caused a gradient to be set up. Thermometers were projected through the cardboard roof. The difficulty with this apparatus was that, owing to the lack of insulation, the temperature gradient within the cage varied with the room temperature. In his work with wood-ants (*Formica rufa*) Herter showed that the temperature of the environment from which the insect was taken influenced its preferred temperature. Figures were quoted which suggested that with an increase in the initial temperature there was a corresponding increase in the preferendum, i.e. that the preferendum varied directly with the temperature of the insect's previous habitat.

Parker (1924), in his work on the clear-winged grasshopper (*Camnula pellucida*), placed fifty first and second instar nymphs on a covered glass plate which was heated in the centre by an electric lamp from below. The temperature ranged from 60° C. above the lamp to 18° C. at the edge of the glass. The grasshoppers arranged themselves in a definite circle around the central area at a temperature of 37–38° C. The experiment was repeated several times. In connexion with an insect's preference for *radiant heat* mention should be made of the early work of Lodge (1918). In working on the sense reactions of house-flies it was observed that they congregated in large numbers round a lighted bunsen-burner and arranged themselves in a very definite circle, the size of which varied according to the distribution of heat. The temperature of this circle was 42–44° C. Heat distribution was controlled by placing larger or smaller pieces of asbestos over the flame, when the flies arranged themselves in larger or smaller circles respectively. If the gas was turned off the flies ceased to sit in a ring, but came closer to the base of the burner.

Kirkpatrick (1925), working with mosquitoes (*Culex pipiens*), provided them with water in troughs on top of a bar of aluminium heated at one end. The water varied from 14 to 36° C. and the females showed a decided preference for water at temperatures of 21–23° C. for oviposition.

Bodenheimer & Schenkin (1928) repeated Herter's early experiments with several insects. They found that the flour weevil (*Tribolium confusum*) had a preferendum of 24·760–26·568° C. if previously kept at a temperature of 15–18° C. However, beetles kept for a month in a constant temperature of 25° C. preferred a zone between 9·118 and 10·740° C. They also found that the average preferred temperature of nymphs of the house cricket (*Gryllus domesticus*) was 20·40° C. in Palestine; while Herter gives 26·512° C. to be its preferendum for Germany. As will be noticed the temperature readings were made to the third decimal place; this seems unjustified since, in most cases, the insect's preferred zone covered several degrees.

Fulton (1928), working independently, devised a preferred temperature apparatus based on an entirely different principle. A trough filled with wet sand was packed in ice at one end, while the opposite end was heated by electric lamps. The wet sand conducted the heat sufficiently well to form a temperature gradient although the changes were greater near the ends. Insects were placed in a glass tube which was imbedded in the sand leaving only the top exposed. Thermometers were pushed into the sand in a slanting direction so that the bulbs were under and in contact with the glass tube. Using adult click beetles (*Melanotus communis*), Fulton found that 57 % came to rest within the range of 26–29° C. The larvae showed no marked preference for any temperature between 17 and 29° C.

Bodenheimer's (1929) work on the desert locust (*Schistocera gregaria*) comprised all stages of the insect. In the development of the young there was a progressive increase in preferred temperature from 29·4° C. for the first stage

nymphs to 36·7° C. for the fifth stage nymphs. Bodenheimer concludes that this rise in the preferred temperature is connected with physiological changes in the insect during development, and also suggests that it is possible that this is connected with the water contents of the insect's body.

Grossman (1929) describes the results of his experiments with the Mexican cotton boll weevil (*Anthonomus grandis*). For this work he employed an apparatus which consisted of a 3 ft. length of $\frac{1}{2}$ in. glass tubing placed within a slightly shorter tube 2 in. in diameter. The space between the smaller and larger tubes was filled with water and sealed off with a cork at the ends. By heating the water at one end of the apparatus and chilling it at the other, a temperature gradient extending from 9 to 60° C. was obtained in the inner tube. In these experiments the weevils only reacted by avoiding temperatures above 49° C.

Bodenheimer & Klein (1930), working with ants, arrived at the conclusion that the preferendum of each species remains practically constant in different months regardless of the differences in the environmental temperatures. Hertzer (1930), working on the behaviour of the Argentine ant (*Iridomyrmex humilis*), used a rather crude temperature apparatus. It consisted of a galvanized pan, 3 ft. long, the bottom covered with soil, with a jar of ice at one end and an electric lamp at the other. The temperature gradient ranged from 13 to 50° C. Using worker-ants with pupae he found that the ants would settle down with their young between 21 and 27° C.

In further illustration of an insect's previous environment affecting its preferred temperature the work of Bodenheimer (1931) may be cited. He suggested that the humidity of the air in which insects are kept before an experiment has an effect on their preferred temperature. For instance, the Tenebrionid beetle, *Adesmia clothrata*, when kept in moist air before an experiment, preferred a temperature of 39·4° C., but when previously kept in dry air, preferred 36·6° C. Gunn (1931) obtained similar results using the cockroach (*Blatta orientalis*). Fahmy (1931) constructed a replica of the original temperature-preference apparatus used by Williams in Egypt. Working with *Ptinus tectus* he found that they preferred a temperature varying from 22 to 25° C. with an average of 23·5° C.

Uvarov (1931) has reviewed the literature on insect preferendum. He states that temperature preferendum 'is probably one of the most potent factors influencing the ecological distribution of insects and their movements', and suggests that the preferendum should be determined for each stage of every insect of economic importance. Nieschulz (1933, 1935) gives a useful discussion on the subject of optimum and preferred temperatures. He investigated the reactions of *Stomoxys calcitrans* to various temperatures. The average optimum was found to be 27·7° C. for the female and 28·8° C. for the male. The relative humidity of the atmosphere was said to be of negligible influence. This optimum temperature was about the same as that at which the normal activity started

to increase. It was found the results were not affected by atmospheric humidity, sex, age, amount of feeding, or egg maturation. The preferred temperature of *Stomoxys calcitrans* was found to average 29·4° C. for freshly captured females and 25·9° C. for males. For females of *Culex pipiens* that had hibernated in a cellar the temperature preferences was 8·9° C.

The following is a comparison of the results obtained by Nieschulz on the reactions of *S. calcitrans* to temperature:

Optimum temperature °C.		Preferred temperature °C.	
Males	Females	Males	Females
28·8	27·7	25·9	29·4

The preferred temperature for the males is almost 3° less than their optimum temperature, while for the females it is 1·7° more than their optimum temperature. These facts are pointed out here since so few investigators of preferred temperature have ever conducted experiments on optimum temperature so that comparisons might be made. Experiments were also carried out by Nieschulz with *Musca domestica* and *Fannia canicularis* similar to those with *Stomoxys calcitrans* above. Optimum temperature for *M. domestica* showed an average of 33° C. for females and 34·2° C. for males. The optimum for both sexes of *F. canicularis* was 23·7° C. A comparison of these results with those for *S. calcitrans* shows that all three flies have typical optimum temperatures that are peculiar to the species.

Martini & Teubner (1933), working with mosquitoes, found the preferred hibernation temperatures were 6–8° C. for *Anopheles maculipennis* var. *messeae* and 10–13° C. for *A. maculipennis* var. *atroparvus*. In the field the former also appeared to avoid high temperatures and high saturation deficiencies more than the latter. Here there was a considerable difference in choice of temperature even between two varieties of the same species. In 1934 Nieschulz carried out further experiments on the temperature preferred by *Stomoxys calcitrans*, the results of which confirmed those published the previous year.

The most exact study of preferred temperature is found in the work of Gunn (1934) on the cockroach. In his experiments he used a temperature-gradient apparatus in the form of a copper trough electrically heated at one end and cooled by ice at the other. The entire trough was well insulated, so that a constant gradient could be maintained irrespective of the room temperature. With this apparatus it was found that the preferred temperature range of an adult male *Blatta orientalis* was 20–29° C., and that this temperature range was not affected by changes in the air humidity.

Herter, in his later work (1934, 1936), used a modified form of his original apparatus in which he inserted thermometers into the aluminium bar, or floor of the gradient. With this apparatus he found the preferred temperature

(which he calls thermotactic optimum) for the flea, *Archaeopsylla*, to be 34·4° C., and for *Cimex*, 35·7° C. These figures are said to agree well with the surface temperature of the insect's hosts. Hertex also experimented with small mammals. Using mice and bats it was found the smaller forms had the higher temperature preference. Results with long-eared bats indicate that the ear perhaps plays a role in temperature perception and so indirectly is a factor in determining the animal's preferred temperature or 'thermotactic optimum'. Herter also recorded the frequency with which orientation occurred with the head toward the cool or heated end of the apparatus.

Nicholson (1934), in working on the influence of temperature on sheep blow-flies, determined the preferred temperature in a different way. The number of flies on the corks of the observation jars at various temperatures was recorded, and it was observed that this number was greatest near the extremes of temperature. Because of their low conductivity the corks probably felt warmer at very low temperatures and cooler at high temperatures, thus being less uncomfortable than the rest of the jar. In these experiments the greatest number of insects gathered on the corks at temperatures below 20° C. and above 35° C. Thus the range between 20 and 35° C. was considered to be the preferred temperature.

Continuing his work on the cockroach, Gunn (1935) made a comparison of the temperature preference of three different species. He found the upper limit of preferred temperature for *Periplaneta americana* and *Blatella germanica* to be 33° C., while for *Blatta orientalis* it was 29° C. The lower limit was not so sharply defined and it was suggested that further work be done before it could be regarded as significant.

Thomsen & Thomsen (1937, 1938) determined the preferendum of certain Dipterous larvae in their natural habitat. The temperature gradient apparatus used allowed the larvae to move freely in dung with a temperature range from 9 to 50° C. This overcame two serious weaknesses of the usual preferred temperature experiment: (*a*) the insects were in their natural medium and had access at all times to their food, (*b*) the relative humidity was fairly uniform throughout the apparatus. Larvae of *Musca domestica* in horse dung showed a definite temperature preference, which varied with their age. Larvae that were feeding preferred temperatures between 30 and 37° C., while those ready to pupate preferred temperatures below 15° C. The preference shown by feeding larvae corresponded to that found in their natural habitat in a fermenting manure heap. Within the manure a temperature as low as 15° C. cannot be obtained, hence pupae are to be found in the earth nearby. The optimum temperature for the development of house-fly larvae was shown to be 34° C. Supplementary experiments indicated that the attraction of the arvae to a given zone of the dung layer depended not solely on its temperature, but also on a chemical change therein. This chemotaxis was particularly marked only during the second day of larval life. The authors conclude that

the vertical distribution and movements of the larvae in natural conditions depend chiefly on their temperature preference and to a lesser degree on chemotaxis, negative phototaxis, hygrotaxis and thigmotaxis.

Larvae of *Stomoxys calcitrans*, which live in litter containing cow dung at 20–30° C., had a preferendum between 23 and 26° C. Comparing the temperature preferences of the larvae of these two species with those obtained above by Nieschulz for the adults it will be seen that the same differences hold. Namely, *Musca domestica* prefers a higher temperature in both the larval and adult stages than does *S. calcitrans*.

The first attempt to determine the preferred temperature of soil insects was made by Campbell (1937) in his work on wireworms. A modified form of Fulton's temperature-preference apparatus was constructed in which wet sand was used for the conductivity of heat and cold. The preferendum for these insects was lowest (17–23° C.) in the period February and March. During the summer the preferendum rose until the high point (27° C.) was reached in September, and then dropped in the latter part of September and October. In general, the experiments indicated that the preferred temperature varies with the season, being higher in the summer and autumn than in the winter and spring. It was also shown there is a lag behind the natural soil temperature, indicating that the preferendum does not change until the wireworms have been subjected to the higher or lower temperatures for a month or more.

Thomson (1938) used an alternative chamber to determine the reactions of mosquitoes, *Culex fatigans*, to temperature and humidity. This apparatus was roughly of the same principle as that used by Gunn & Kennedy (1936) to determine the reactions of insects to humidity. The maximum difference of temperature between each side of the chamber was only 10° C. All stages of the mosquitoes showed a strong avoidance of high temperatures. This was strongest in the hungry females, less strong in the blood-fed females and those with mature ovaries, and least strong in the newly emerged females. Gunn & Cosway (1938) tested cockroaches for their preferred temperature at two different humidities—moist and dry. In general, the average preferred temperature of these insects was higher in moist air than in dry. Individual cockroaches which did not react to humidity at a constant temperature likewise ignored the humidity in a temperature gradient. However, individuals which did react to humidity at a constant temperature also reacted to it in a temperature gradient by going to a lower temperature in dry air than they did in moist.

The only work on the reactions of aquatic animals to a temperature gradient is a recent paper of Doudoroff's (1938) on fishes. An apparatus is described whereby a steep horizontal temperature gradient can be maintained without the presence of vertical gradients in the water. Several species of marine fishes, chiefly *Cirella nigricans*, showed a marked selection for temperatures which were relatively high in comparison with the normal environment of the

fishes. While acclimatization was found to influence selection, the effect was slight and only temporary, the selected temperature being, to a large extent, independent of past experience. It was concluded that selection is indicative of the relative stimulative or detrimental effects of given rapid changes of temperature, while the common view that such selection indicates the nature of 'optimal' conditions or habitat preference is not tenable.

3. Description of temperature gradient apparatus

Since the various pieces of apparatus used in the present work are new, or modified, a brief description is necessary. It should be mentioned that all were made in the Rothamsted workshop and were relatively inexpensive. The total cost of the two most expensive items, the linear brass gradients, was under £2 each.

(*a*) *Williams's early apparatus*

Plate 9A is a photograph taken by Dr C. B. Williams of his original temperature-preferendum apparatus. When the present work was started, the first temperature gradient to be constructed and tried was a replica of this. It consisted of a glass tube 1½ in. in diameter and 40 in. in length, supported at each end by a retort stand with clamps. 'Compo' tubing, ¼ in. in diameter, was tightly coiled in a spiral fashion about the glass tube and looped down at one end with a small gas flame on the steep slope. At one side both ends of the compo tubing were joined to a Y tube, which in turn was joined to a glass funnel by means of rubber joints. This funnel was for filling the coils with water. In order to prevent air locks no water was used in the coils which had not previously been boiled. Compo tubing of a low melting point, which cannot be passed directly into a flame, should be immersed in a hot water bath which in turn may be heated by a bunsen burner. For taking temperatures a thermometer, with a thread tied to each end, was inserted into the glass tube and the strings allowed to hang free at the ends. The thermometer could thus be pulled along in either direction and the temperature recorded at any position in the apparatus where insects were gathered. The ends of the glass tube were plugged with cotton wool.

By heating the water at one point and setting up a circulation through the compo coils, a gradient could be maintained from a high temperature (about 35° C.) at one end of the apparatus down to room temperature at the opposite end. Inversely, if the compo loop were cooled instead of heated a gradient could be made from a low temperature at one end up to room temperature at the other end.

The great advantage of such an apparatus was that an insect had at all times a choice of a series of gradients. Each space between two compo coils offered a small independent gradient. Above the preferred temperature the insects tend to group in the cooler space between the coils, and below the preferred temperature in the warmer area on the coils. After a few trials, this apparatus was abandoned in a search for one which offered a complete gradient from a low to a high temperature.

(*b*) *Brass trough with ice-box* (Pl. 9B and Fig. 1)

This apparatus was made in the form of a trough built up from solid brass strips ½ in. in thickness. The inside depth was 1 in., the inside width 2 in., and the overall length 4 ft. The trough was blocked off 3½ in. from each end by soldering in place a brass piece of the same thickness as the sides.

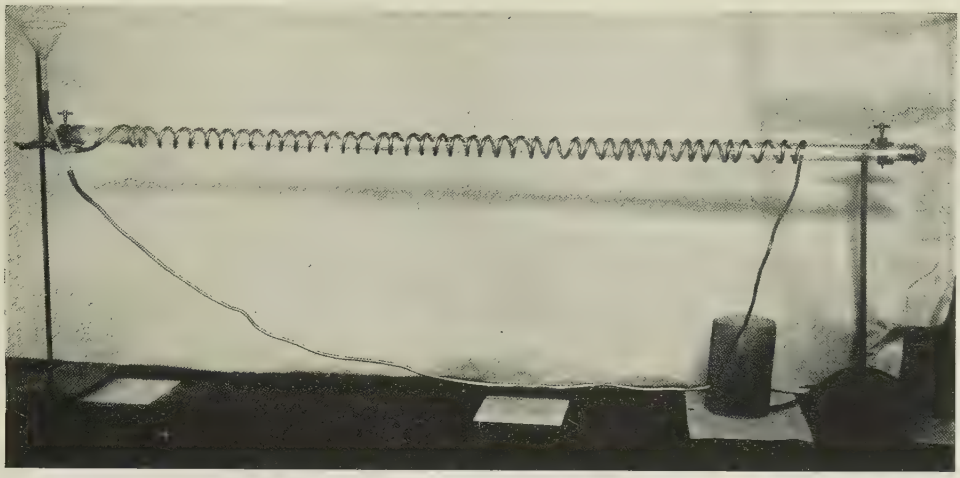

Photo A. Apparatus used by Williams in 1923.

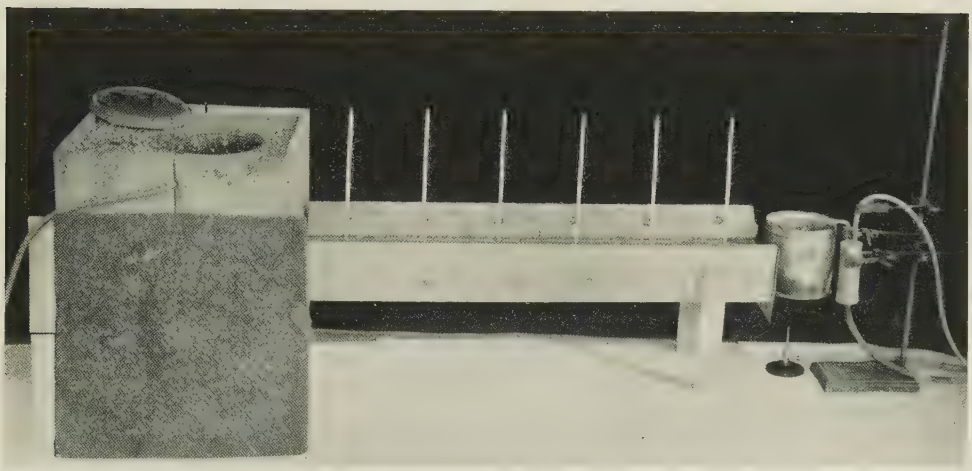

Photo B. Gradient apparatus with hot bath and ice-box. (Thermometers 6 in. apart.)

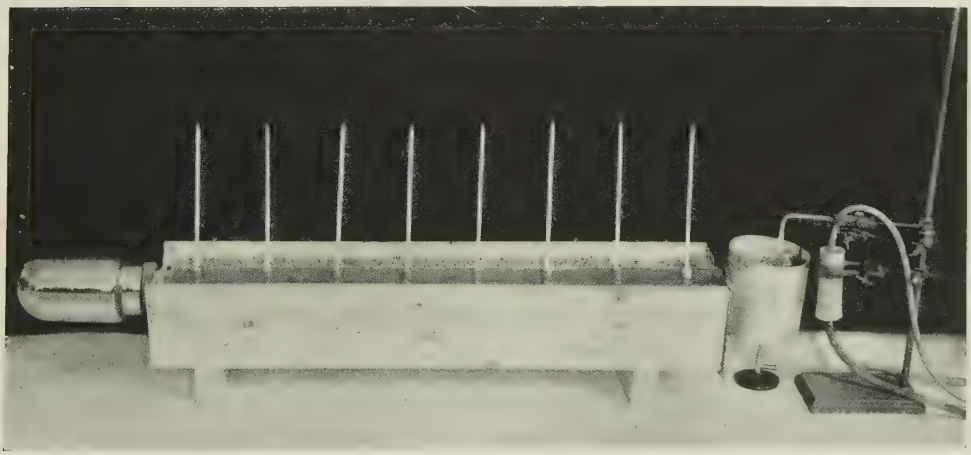

Photo C. Gradient apparatus with hot bath and Thermos jar. (Thermometers 5 in. apart.)

Face page 330

A circular tin 6 in. in diameter by 6 in. in depth was secured and a hole made into one side 2 in. from the bottom. The trough was projected through this opening into the tin for a distance of 3½ in., and the tin soldered tightly about the brass end-piece. This was to serve as a hot water bath for heating the hot end of the gradient.

For the other end of the trough a larger tin was secured (a 28 lb. honey pail), 8 in. in diameter by 12 in. in depth, and with a tightly fitting cover. A hole was made in the can 2 in. from the bottom and the free end of the trough projected into the tin the same distance as for the opposite side, and soldered in a like manner. Since this honey pail was to store the ice for the cold end of the gradient good insulation was necessary. First it was wrapped with cotton wool. Then a wooden box, 18 by 18 in. and 21 in. deep, was built around it so that the top of the tin was just level with the top of the box. The box was filled with granulated cork, which was firmly packed about the tin. Near the top of the tin was fitted an overflow outlet so that the water from the melting ice could drain off. The entire box was then covered with a square of thick felt as used for covering bee hives, and over this was a wooden lid.

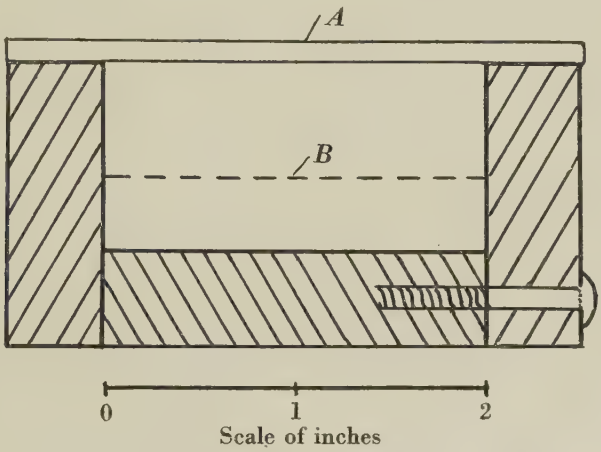

Fig. 1. Cross-section of linear apparatus. *A* = glass top. *B* = false floor of organdie.

There was thus left an actual run-way in the trough of 37½ in. for the insects. (Notice that 3½ in. of the gradient which ran from the ice chamber to the outside of the insulation box was lost for experimental work.) In order to prevent temperature loss from the metal gradient it was also lagged in the same way as was the ice container. First with cotton wool and then with granulated cork. To hold the cork a wooden trough 8 in. wide and 4 in. deep was built to fit about the entire exposed length of the brass channel. At the cold end this trough fitted flush with the ice-box, while at the hot end it was covered with tin-plate to protect it from the bunsen burner.

The cover to the gradient consisted of six glass plates each 6¼ in. long, 3 in. wide, and ⅛ in. in thickness. The ends of each plate were ground so as to fit tightly to the next and a hole was drilled in the centre of each to admit a thermometer. The glass covers were then sealed in place with vaseline. The rubber stoppers used to hold the thermometers in position were first 'weathered' out of doors for 3 months. This was to avoid any toxic emanation from the new rubber as discussed by Mellanby & Buxton (1935). A piece of wall board ½ in. thick, 3 in. wide, 38 in. long and with holes bored to allow for the thermometers to project through was then placed over the glass. The primary purpose of this cover was to darken completely the experimental chamber whenever this was desired. However, it was also

beneficial in serving as additional insulation. A 95 cm. rule was placed alongside the trough for determining the position of the insects.

The hot water bath was kept at a uniform level (about 1 in. from the top of the tin) by means of a constant level apparatus (Fig. 2). This was held in place by a retort stand and was supplied with a constant stream of water from a nearby tap with an overflow to the sink. The heat for the water bath was supplied from a micro bunsen burner which was fitted to burn night and day.

With this apparatus a temperature gradient over a 3-day period (the length of each experiment) averaged from about 10° C. at the cold end, when cooled with ice and salt, to 35° C. at the hot end. There was but little variation from hour to hour except at the cold end, which fluctuated between 5 and 10° C. The temperature gradient was approximately a straight line allowing the insects a choice of about 1° C. in every 4 cm.

(*c*) *Brass trough with Thermos vacuum flask* (Plate 9 C)

This apparatus was also of brass and was constructed in practically the same way as the above gradient. The only difference being that the ice for the cold end was contained in a 1 gallon Thermos vacuum flask instead of a lagged ice-box. One end of the trough was projected through the flask's cork for 4 in. and the cork sealed in place about the trough with marine glue. The flask could then be filled with ice and salt and slipped on and off the cork at the end of the gradient.

By using the vacuum flask, and thus eliminating the large amount of lagging, an additional $2\frac{1}{2}$ in. of the trough were made available for experimental purposes. This gave a runway of 40 in. instead of $37\frac{1}{2}$. To cover this trough eight pieces of glass, 5 in. in length (and eight thermometers), were used instead of six as in the previous gradient (Fig. 3).

Ice remained in the flask for a period of 24 hr. However, when the ice was not in actual contact with the brass bar the temperature immediately went up at the cold end of the gradient. To avoid this a larger Thermos would probably be of advantage. Otherwise the gradient obtained was about the same as when an ice-box was used.

The chief advantages of this apparatus were as follows: (*a*) light in weight —easily moved about by one person, (*b*) compact, took up less space, (*c*) used a minimum of ice. This gradient machine was not constructed until near the end of the preferendum work and no results from it are included in this paper.

4. Technique of experiments

(*a*) *Apparatus and working precautions*

So far as I am aware only one previous worker on thermo-preferendum has ever made any attempt to distinguish between floor temperature and air temperature in the gradient. Most have taken the air temperature by projecting thermometers through the top, or sides, of the apparatus while the insects remained in contact with a metal floor. In the present work it was decided to test the gradient for any possible differences in temperature within the apparatus itself. The following are the average results of twenty readings

taken at three different positions along the linear gradient, i.e. at 85 cm. the cold end; 55 cm. the centre of the gradient; and 10 cm. the hot end:

Position in gradient	Floor	Centre	Roof
85 cm.	6° C.	11° C.	11° C.
55	20·5	21	21
10	44	36	36

The average room temperature was 20° C. 'Floor' indicates that the thermometer was lying flat on the floor but the bulb was not in metallic contact with it. 'Centre', the thermometer bulb was projected through the glass cover, to about midway in the apparatus, in the same position as when experimental temperature readings were taken. 'Roof' indicates that the thermometer was propped tightly against the inside of the glass roof. All three thermometers (i.e. floor, centre and roof) were placed in tier one above the other at each of the three positions shown above.

As can be seen at the cold end the floor was 5° colder than the centre and roof. In the centre the floor, centre and roof temperatures were all about the same. This was more or less expected, since the temperature here was approximately the same as that of the room. At the hot end the floor was 8° hotter than the air above it or the roof. In no single reading was the difference between either the centre or air temperature and the roof ever more than 0·5°, the average being the same for both.

In order that the air surrounding the insects should be as nearly as possible at the same temperature as that recorded on the thermometers, and in order to avoid any controversy on the subject, a false floor was placed in the apparatus. This floor was of finely woven 'organdie' cloth and was held in place, half-way between the brass floor and the cover, by adhesive zinc-oxide plaster. This plaster had no apparent odour and was superior to all other sticking substances in preventing even the smallest insects from working their way beneath the cloth. It was later discovered that this false floor had the following additional advantages: (*a*) it was easy to see the insects against a white background, (*b*) the insects could easily get a foothold, (*c*) if any insects got on to their backs they could readily right themselves.

Thermometers were placed at 10, 25, 40, 55, 70 and 85 cm. In the early experiments temperature readings were taken every 30 min., but since there was little variation in the temperature the readings were reduced to one each hour in the later work. At each temperature reading a record was also taken of the room temperature. Since most of the insects experimented with had a preferred range of several degrees all temperature readings were taken to the nearest degree only, never to fractions.

It is impossible to have a temperature gradient without also having an inverse gradient in relative humidity, i.e. the relative humidity will be the lowest at the warm end of the gradient and highest at the cool end. The only

way to maintain a constant relative humidity in a temperature gradient would be by completely drying the air or by keeping it saturated. Since neither of these alternatives appeared feasible it was decided to measure and record the relative humidity each day. In this linear gradient it varied from 10 to about 45 %. However, as will be shown later, it was possible to keep an approximately uniform relative humidity when the experimental trough was filled with food for certain stored product insects.

Since the space above the false floor was only $\frac{1}{2}$ in. in height and 2 in. in width the relative humidity had to be taken with a very small instrument. For this purpose four Edney paper hygrometers were selected as used by Gunn & Kennedy (1936). These are watch-like instruments, 2 in. in diameter and about $\frac{1}{4}$ in. in thickness, and give a direct reading of relative humidity. They were placed in the apparatus at night, after the insects had been removed, and the relative humidity recorded the following morning. They thus had ample time to reach equilibrium before the readings were taken. The hygrometers were always placed at 0, 30, 60 and 90 cm. along the gradient. Each week the hygrometers were calibrated with a wet and dry bulb sling psychrometer. In addition, during the day, when not in use, they were kept in separate desiccators in which the relative humidity was controlled by known concentrations of sulphuric acid as described by Buxton & Mellanby (1934). Each hygrometer had a number, and the one used at the dry end of the gradient was kept at a low humidity (about 10 %); the one used at the moist end was kept at about 75 % relative humidity and the remaining two at intermediate humidities.

In very few of the papers on thermo-preferendum has the humidity ever been measured or even mentioned. Nieschultz (1933) made an attempt to overcome the humidity difficulty by having desiccating agents at the cool end and humidifying solutions at the warm end of the apparatus. Gunn (1934) forced a regulated stream of air of a known dew point into his apparatus. More recently Thomson (1938), working with mosquitoes, determined the humidity range to which they were insensitive and then kept his temperature gradient within this predetermined zone. However, with mosquitoes this was quite easy to do, since all stages were indifferent to a relative humidity between 30 and 85 %.

The hot water bath was kept heated by a gas flame day and night, and the ice-box was likewise kept continually packed with ice. A uniform gradient could thus be maintained continuously over a period of weeks or even months. The advantages of keeping the gradient going over long periods were: (*a*) one could commence work immediately upon arrival in the morning without waiting for a gradient to form, (*b*) the hygrometers could be left in the apparatus over night for recording the relative humidity at different positions along the gradient. The ice-box was packed three times a day, morning, noon, and night, with two parts finely crushed ice and one part common salt (sodium chloride).

This mixture gives a theoretical temperature of −18° C. according to Kaye & Laby (1921). An average of about 6 lb. of ice was used at each packing. In order to secure the maximum results from this freezing mixture it was necessary to keep the water level about 2 in. above the brass trough which projected into the ice-tin. The water above this level was periodically siphoned off into the sink. About once a month the salt which caked at the bottom of the tin also had to be cleaned out.

The first experiments were conducted in a laboratory with three south windows. Although the windows were shaded it was quite impossible to keep the light uniform on all parts of the gradient. During the same day the light might change from bright sunshine to cloudiness and at night to artificial light. The experimental trough was therefore kept completely dark by covering it with 'masonite' wall board cut to fit exactly over the glass plates. However, when the cover was lifted for the purpose of making an observation, the insects immediately became restless, and started moving about. After a little preliminary work, all apparatus and experiments were moved to a dark room in the basement. During each experiment only one small shaded light was alight, and this was below the level of the trough. An indirect uniform dim light, which was just sufficient to see the position of the insects, was cast over the gradient. This dark room had an additional advantage in that it was constructed as a constant-temperature room. Although no attempt was made to keep it at a uniform temperature it nevertheless remained between 18–21° C., night and day, throughout the year.

It should be mentioned that each time work was started with a different species of insect the gradient was thoroughly sponged out with cotton wool and boiling water, and the false floor removed and replaced with a new one.

(*b*) *Observations*

Each experiment was carried on for a period of 3 days. The number of observations made varied somewhat according to the nature of the experiment, but usually every half-hour the number of insects, and their positions in centimetres, were recorded. When insects were used with food, observations were made after they had been in the gradient for 1 hr., 2 hr., 4 hr., 8 hr., etc. This was to see how long it took the insects to come to their preferred temperatures and if their preference changed with time. After each experiment a control was carried out for 1 day at a uniform temperature. This was for the purpose of getting the random distribution of the animals when there was no gradient. A control often showed an insect to be strongly thigmotropic (for example, the bed-bug), or to have definite end preferences. So far, the Thomsens have been the only experimenters to use a control in connexion with preferendum work.

Thirty insects were usually used in each experiment, five being introduced into each of the six cover openings. Half-hourly observations usually resulted

in twenty-four readings a day, seventy-two in 3 days. Thus there was a total of 720 observations daily or 2160 for the 3 day experiment. The numbers of insects, both experimental and control, were all originally plotted against position in centimetres, and, superimposed upon this, the temperature and humidity were also plotted against position (Fig. 2).

Taking the insects' positions in centimetres rather than recording the number at each temperature had the following advantages: (*a*) it permitted the rapid recording of observations, and no interpolation between thermometers was necessary; (*b*) it allowed the plotting of experimental results

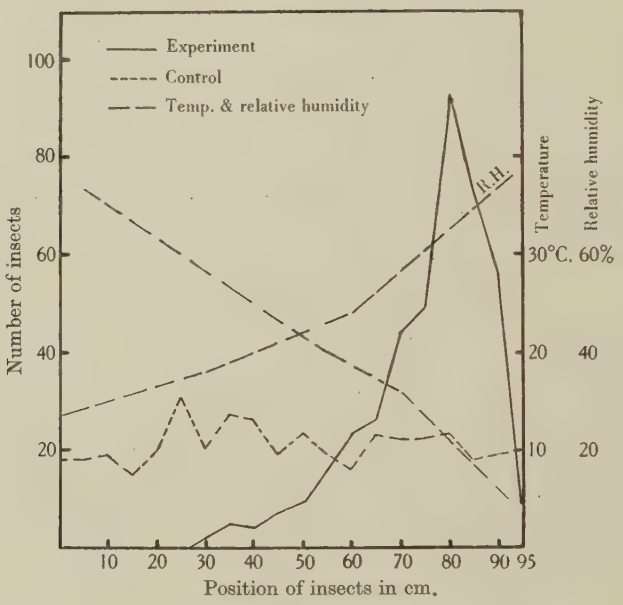

Fig. 2. Temperature-preference curve of adult *Apanteles congestus* (Braconidae, Hym.) arranged according to position in centimetres in the gradient. Each point is the average of not less that forty-two hourly observations on thirty insects previously kept at room temperature (cf. Fig. 3).

against a control—since the control was taken in centimetres at a uniform temperature, positions had to be taken in centimetres; (*c*) it is easy to convert position into temperature gradient, but more difficult to record the reverse process; (*d*) some insects may have an end preference which would not show up if positions were taken in °C.; (*e*) the results lend themselves more readily to statistical treatment; (*f*) some insects may not respond to a change in the temperature gradient; but if their positions were taken in °C. and the temperature gradient changed, they would appear to be changing their preference —when in reality it would be the temperature changing and not the insects.

If we have insects which distribute themselves evenly (i.e. no preference) in a gradient that is high at one end, low at the other and fairly uniform in the

centre, and if these insects were plotted against position, a straight line would result. If plotted directly against temperature, a curve would be obtained with a central mode, apparently indicating that these insects had a temperature preference for the centre of the apparatus, merely because a longer space at each temperature would be available in the middle. It would not show the even distribution of the insects nor that just as many per centimetre were at the hot and cold ends as were in the centre.

The difficulty of showing all results in this form is that each experiment requires a separate graph. When they are converted into numbers of insects against temperature this resulting graph is as shown in Fig. 3. This form has been used for a selection of results, as a larger number can be illustrated in a small space.

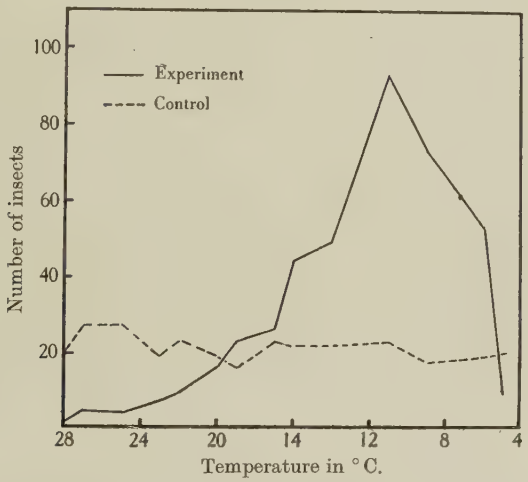

Fig. 3. Temperature-preference curve of adult *Apanteles congestus* (Braconidae, Hym. arranged according to temperature in gradient in °C. (cf. Fig. 2).

The original records were taken in the manner shown in Table 1. It is impossible to print all of these; but the original records are deposited at Rothamsted Experimental Station, where they can be consulted.

(*c*) *Insects used*

A total of twenty-three species of insects from six orders has been tested for their temperature preferendum. These have included insects of widely different environments and habits, such as the following: stored product insects, leaf-feeding insects, plant-sucking insects, human parasites, insect parasites, and soil insects. During the winter months work was done on stored product insects (mainly beetles), while in the warmer months insects from out of doors were used. The summer insects included such pests as ants,

Table 1. *Example of daily records kept for experiments using linear apparatus*

Exp. no. 36. Insect: *Apanteles congestus*. Stage of insect: adult. No. of insects: 30. Temperature previous habitat: 20° C.

Cm. ...	.. ...	0	30	60	90	10	25	40	55	70	85	Room	0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90
		% rel. hum.				Temperature °C.							Position of insects																		
Date	Time																														
Sept. 12	9 a.m.	33	40	50	73	35	30	25	20	15	10	20			5			5			5			5			5			5	
	10 a.m.	.	.	.	.	35	30	25	20	15	10	20	.	.	.	.	.	.	2	3	4	1	.	2	4	.	6	2	7	.	.	.
	11 a.m.	.	.	.	.	35	30	25	20	15	10	20	.	.	.	.	.	.	2	2	3	.	.	3	3	1	8	.	6	2	.	.
	12 noon	.	.	.	.	35	30	25	20	15	10	20	.	.	.	1	.	.	1	2	.	3	.	3	5	2	5	.	5	3	.	.
	1 p.m.	.	.	.	.	36	31	26	21	16	9	21	.	.	.	.	.	.	.	1	.	6	.	3	6	2	4	2	6	.	.	.
	2 p.m.	.	.	.	.	36	31	26	20	15	8	21	.	.	.	.	.	.	.	.	1	.	3	4	4	3	6	4	5	.	.	.
	3 p.m.	.	.	.	.	36	31	26	20	14	7	21	.	.	.	.	.	.	.	.	.	1	4	1	8	4	.	3	5	4	.	.
	4 p.m.	.	.	.	.	36	30	25	20	14	7	21	.	.	.	.	.	.	.	.	.	.	2	4	7	2	3	3	8	1	.	.
	5 p.m.	.	.	.	.	36	30	25	20	14	7	21	.	.	.	.	.	1	.	.	.	2	2	2	4	2	4	3	8	2	.	.
	6 p.m.	.	.	.	.	36	30	25	20	14	7	21	.	.	.	.	.	.	.	.	.	.	3	3	3	3	4	5	5	4	.	.
	7 p.m.	.	.	.	.	36	30	25	20	14	8	21	.	.	.	.	.	.	.	.	.	.	2	2	2	3	6	6	6	3	.	.
	8 p.m.	.	.	.	.	36	30	25	20	15	8	21	.	.	.	.	.	.	.	.	.	.	.	2	2	4	6	4	7	5	.	.
	9 p.m.	.	.	.	.	36	30	25	20	14	7	21	.	.	.	.	.	.	.	.	.	.	.	.	3	5	5	6	8	3	.	.
	10 p.m.	.	.	.	.	36	30	24	19	13	6	21	.	.	.	.	.	.	.	.	.	.	.	.	3	7	5	11	3	1	.	.
	11 p.m.	.	.	.	.	35	29	24	19	13	6	20	.	.	.	.	.	.	.	.	.	.	.	.	2	6	4	7	6	4	1	.
						35·7	30	25	20	14·4	8	20·7	0	0	0	1	0	1	5	8	8	13	16	29	56	44	66	56	85	32	1	0

wireworms, sawflies, earwigs, etc. The following is a detailed list of the species used.

Order	Family	Species
Dermaptera	Forficulidae	*Forficula auricularia* Earwigs
Hemiptera	Cimicidae	*Cimex lectularius* Bedbug
	Pyrrhocoridae	*Dysdercus howardi* Cotton stainer
Lepidoptera	Tineidae	*Tineola biselliella* Common clothes moth
Coleoptera	Elateridae	*Agriotes* sp. Wireworms
	Bruchidae	*Acanthoscelides obtectus* Bean weevil
	Ptinidae	*Ptinus tectus*
	Anobiidae	*Lasioderma serricorne* Tobacco beetle
		Sitodrepa panicea Biscuit weevil
	Curculionidae	*Calandra granaria* Granary weevil
		Calandra oryzae Rice weevil
	Dermestidae	*Dermestes vulpinus* Leather beetle
		Anthrenus verbasci Carpet beetle
	Tenebrionidae	*Tribolium confusum* Confused flour beetle
		Gnathocerus cornutus Horned flour beetle
		Tenebrio molitor Meal worms
	Cucujidae	*Oryzaephilus surinamensis*
		O. mercator Saw-toothed grain beetles
		Laemophloeus turcicus
Hymenoptera	Tenthredinidae	*Pteronidea melanaspis* Saw-flies
	Braconidae	*Apanteles congestus*
	Formicidae	*Acanthomyops* sp.
Diptera	Sepsidae	Sepsid flies

With many of the insects, both the immature and adult stages were tested separately and the results compared in an effort to find differences, or similarities, in their preferendum. With others the sexes were experimented with independently to see if sex could be in any way related to choice of temperature.

All species experimented with were kept at room temperature. As stated above this remained at 18–21° C. in the dark room. In addition to these, a number of insects were also kept at a high temperature (27° C.) to see if this would alter their preferendum. A constant temperature oven, thermostatically controlled to keep at 27° C., was used for this purpose. Some soil insects were

also kept at low temperatures (freezing) before being tested. A comparison was then made between those previously kept at room temperature and those kept at freezing point.

The technique of previous workers has been to place insects in a preferendum apparatus without food, in a strange environment and often in bright or changing light. (Thomsen & Thomsen (1937), who worked with maggots in dung, are an exception.) In an endeavour to determine if insects react to a temperature gradient in the same way with food as they do without it, several stored product pests were tried. The experimental trough was filled with their usual food (rice, bran, wheat, fish meal, etc.) and the insects distributed in the normal way. The glass cover to this linear trough was cut into six sections of 16 cm. each. This was a great advantage in removing insects with food, or with soil, since only two 8 cm. sections needed to be uncovered at a time. All twelve sections of food were removed at one time and placed in separate Petri dishes. This was to avoid any movement of insects, due to a change of temperature, when the apparatus was opened. This same technique was used for determining the position of soil insects along the gradient.

Since the thermometers projected directly into the food material, quite an accurate temperature record was obtained of the insect's actual habitat. An additional advantage in using food was that an almost uniform humidity was maintained over the period of the experiment (3 days). However, it is likely that if the food were allowed to remain in the gradient for a longer period a humidity gradient would have finally been set up.

In selecting specimens for an experiment, only the most active and healthiest ones were chosen. Those that were crippled, deformed or appeared abnormal in any way were thrown out. Each experiment was always carried through to its completion with the same individuals originally selected. For example, if one or two insects died, were lost or killed in the middle of an experiment they were not replaced by fresh ones. This accounts for the total number of observations not being the same in certain of the experiments. After the last observation was made at night the insects were removed from the apparatus and fed in a container separate from the stock supply. In transferring the insects to and from the gradient, they were always handled with a camel-hair brush in order to prevent any injury to them.

An equal number of insects, usually five, was introduced into each of the six thermometer openings. After each observation was recorded the insects were disturbed to see if they would return to a similar temperature. No attempt was made to direct them in any particular direction but just to start them moving. Two methods were used for this. The first was to have within the trough a light piece of bent iron wire which by means of a magnet could be used to disturb the insects from outside the glass cover, as used by Gunn & Cosway (1938). Secondly, insects that were not sensitive to the wire and magnet were disturbed by a thin copper wire, well protected with rubber.

5. RESULTS

(*a*) *Stored product insects* (Table 2)

The flour beetle (*Tribolium confusum*), when kept at room temperature, showed a definite temperature preference for 25 to 30° C. and gradually diminishing down to 10° C. (Fig. 4). In a separate experiment the beetles

Fig. 4. Temperature-preference curves of adult insects of various species previously kept at room temperature (without food).

were kept for a month at a constant temperature of 27° C. (their optimum) previous to going into the gradient. These formed a very high peak at the cold end, 14° C., with the exception of a few that distributed themselves irregularly from 30 to 16° C. (Fig. 5). The peak number of insects thus occurred at a temperature 12° lower than when kept at room temperature. In general these results agree with the work of Bodenheimer (1928) on *T. confusum*.

In discussing extremes of temperatures Chapman (1931) makes the following statement: 'it would seem, in general, that the tropical insects, including

those of tropical origin, do not have the capacity for enduring dormancy. This is true of *Tribolium confusum*, which will die in a few weeks at 7° C.' In view

Table 2

Stage	Previous temp.	Food	Preferred temp. °C.	Preferred range humidity	Figure
Tribolium confusum (Flour beetle)					
A	Room	None	25–30	35	4
A	27° C.	None	(14)	60	5
A	Room	Bran	10–(25–30)	38	6
Lasioderma serricorne (Tobacco beetle)					
A	Room	None	15–32	40–55	4
A	Room	Rolled oats	8–32	45	6
A	27° C.	None	(15) and (27)	40–60	5
Calandra oryzae (Rice weevil)					
A	Room	None	10–20	40–60	4
A	27° C.	None	(14)–23	40–60	5
A	Room	Rice	8–(17)–25	60	6
Calandra granaria (Grain weevil)					
A	Room	None	(14)–25	20–60	—
A	27° C.	None	(14)	60	—
A	Room	Wheat	9–(20)–30	60	—
Dermestes vulpinus (Leather beetle)					
A	Room	None	(30)	60	7
L	Room	None	(30)	60	—
L	Room	Fish meal	20–30	55	—
A	Room	Fish meal	(7)–(16)–(25)	30–36:45	8
Gnathocerus cornutus (Horned flour beetle)					
A	Room	None	13–(20)–35	23–70	—
L	Room	None	13–(20)–35	23–70	7
L	Room	Bran	12–30	35	8
Ptinus tectus					
A	Room	None	(8)	80	—
A	Room	Fish meal	(8)	55	—
Tenebrio molitor (Mealworms)					
L	Room	None	13–(19)–20	25–42	7
L	Room	Bran	13–(19)–20	60	8
Oryzaephilus mercator					
A	Room	None	15–(24)–(28)	—	—
Oryzaephilus surinamensis					
A	Room	None	15–(24)–(28)	—	—
Replicate of above two					
A	Room	None	(10)–(28)	40–70	—
Anthrenus verbasci (Carpet beetle)					
A	Room	None	8–(12)–25	40–45	—
Acanthoscelides obtectus (Bean weevil)					
A	Room	None	13–30	15–40	—
Sitropeda panica (Biscuit weevil)					
A	Room	None	14–(21)	20–40	—
Laemoploeus turcicus					
A	Room	None	14–(17)–(21)–28	30–60	—
Tineola biselliella (Clothes moth)					
L	Room	None	14–(17)–20	30–40	—

A = adult; L = larva.

of the above the insects going from a previously high to the lowest possible temperature could hardly be associated with going to a more favourable habitat.

When given bran in which to move about and feed they still showed a marked preference for 25–30° C.; but there were also more insects at the lower temperatures and even a slight rise at the cold end (Fig. 6). *Tribolium*'s temperature preference in these two experiments corresponds quite closely to their optimum, which is 32° C. for reproduction, according to Chapman (1931).

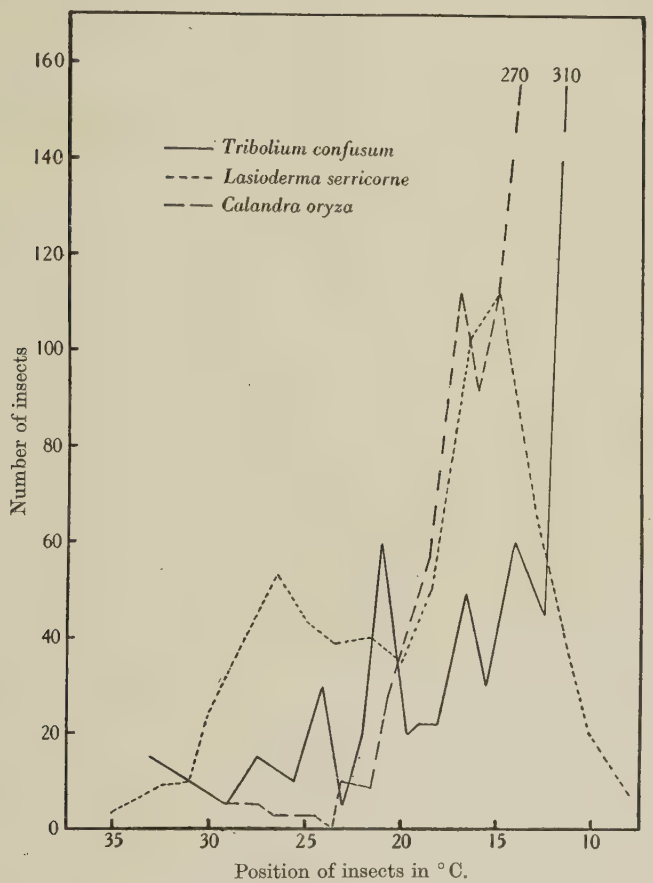

Fig. 5. Temperature-preference curves of insects shown in Fig. 4 but previously kept at a temperature of 27° C. (without food).

The temperature-preference curve for the tobacco beetle (*Lasioderma serricorne*) fluctuates over a zone from 32 to 15° C. (Fig. 4). When given food this zone became even wider, extending all the way from 32° C. to the cold end of the gradient (8° C.) (Fig. 6). However, after being kept at 27° C. for a month the beetle's preference was altogether changed. There was a slight peak at 27° C. and then a very decided one at 15° C. with a complete dropping off at the cold end (Fig. 5). In the first two experiments only about 25 % of the insects were found to be near 32° C.—the temperature given as their optimum

by Powell (1931)—and in the last experiment less than 15 % were near this figure.

Rice weevils (*Calandra oryzae*), previously kept at room temperature, present a violently fluctuating curve rising somewhat at the cool end (Fig. 4). When previously kept at a constant temperature of 27° C. they form a curve beginning at about 23° C. and rising very rapidly at the cool end (Fig. 5). On the other hand, weevils given rice, as a medium in which to choose their temperature, formed a peak at 17° C. which gradually sloped off to 25° C. on one side and 8° C. on the other (Fig. 6). Thus in every experiment these insects were found in greatest numbers at a temperature much below their optimum of 25° C., as given by MacLagan & Dunn (1936).

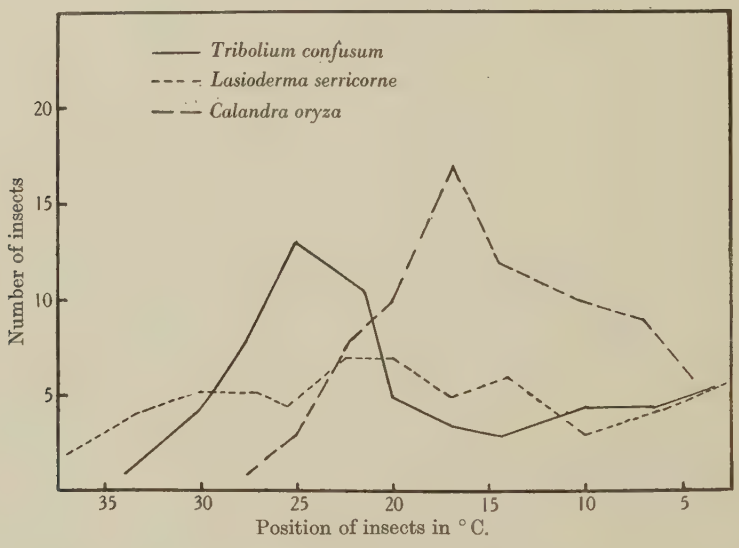

Fig. 6. Temperature-preference curves of insects shown in Figs. 4 and 5 when given food in the temperature gradient.

The temperature preference for the grain weevils (*Calandra granaria*) begins at 35° C., starts to rise at 25° C. and finally makes a very rapid ascent at 14° C., the cold end of the gradient. When the weevils were kept at a constant temperature of 27° C. for a month they gathered in even larger numbers at the cold end. Beginning at about 28° C. the numbers do not increase greatly until the temperature reaches 14° C., then the curve rises almost perpendicularly towards the cool end. When given food, the insects had a definite preference for 20° C., which tapered off to 30° C. on the hot and 9° C. on the cold side. With food, their preference was almost identical to that of *C. oryzae* above. However, in no case were more than about ten insects ever found near 28° C.—their optimum as found by Kunike (1936).

Both larvae and adults of the leather beetle (*Dermestes vulpinus*) behaved similarly in the temperature gradient. After reaching a very steep peak at 30° C. they dropped suddenly and then trailed off in small numbers to 9° C. (Fig. 7). With food the larvae had a rather wide preference zone, extending from 32 to 20° C. with another slight rise at 7° C. Adults with food had three

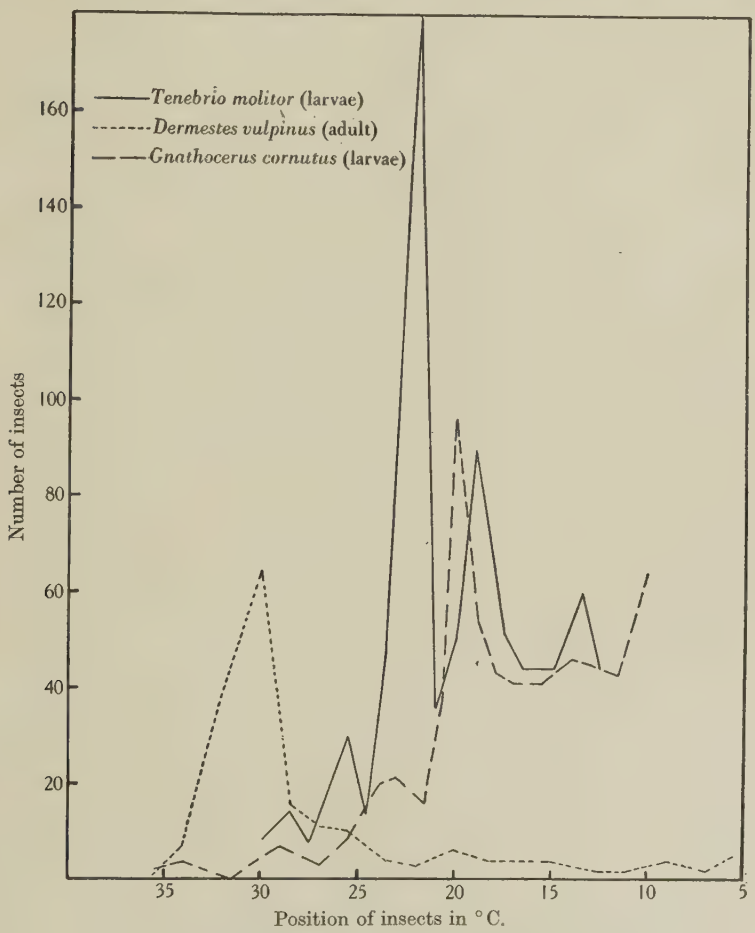

Fig. 7. Temperature-preference curves of certain adult and larval insects previously kept at room temperature (without food).

quite separate and definite peaks; the first one at 25° C., the second at 16° C., and the third at 7° C. (Fig. 8).

There was also a great similarity between the larval and adult temperature-preference curves of the horned flour beetle (*Gnathocerus cornutus*). They both began at about 35° C. and reached their maximum at 20° C., then declined to 13° C. However, the adults rose slightly at the end of the trough. When the larvae were placed in bran they occupied a longer range than before—a range

extending from 30° C. to about 12° C. (Fig. 8). No experiments were conducted with the adults in their food medium.

Both with and without food, *Ptinus tectus* showed a decided preference for the cold end of the gradient—about 8° C. Once, when tested without food, they showed a very weak preference for 25–20° C. *P. tectus* differed from most

Fig. 8. Temperature-preference curves of insects shown in Fig. 7 but with food in the temperature gradient.

insects which went to a low temperature in that they were active and perfectly able to move about at all times. Most insects had to be removed from the cold end before they regained sensibility and could move about. It appears that this species remained in the cool zone because of preference and not because of being trapped. Also in the controls, at a uniform temperature, *Ptinus* distributed itself evenly throughout the length of the gradient.

Meal worms (*Tenebrio molitor*), both with and without food, rose to their highest peak at about 20° C. (Figs. 7 and 8). Without food, they had a minor

peak at 19° C. and another at 15° C. On the other hand, when food was supplied, there was a gradual decline from their maximum to 9° C. at the cold end. It might be suggested that the meal worms tested first left an odour, thus causing those in the second experiment to gather in the same place. This would hardly seem possible, since the first experiment was conducted on 19–21 April and the second on 29 November–1 December 1937. It is rather surprising that even more larvae were not found near the cold end, since they can survive cold much better than heat. Cotton & St George (1929) found that all stages of the meal worms were killed by a 1 hr. exposure to 52° C., while larvae exposed for more than 7 months to a freezing temperature remained alive.

A comparison between experiments with the saw-toothed grain beetles (*Oryzaephilus mercator* and *O. surinamensis*) showed the preference of both species to be almost identical, with two definite peaks. Here the two peaks were quite close together, one at 28° C., while the other was 24° C. The results for *O. mercator* were obtained from experiments conducted 5–7 March, while *O. surinamensis* was not tested until 19–21 March. In the presence of such striking similarities, it was decided to repeat the experiment at a later date. A replicate was started on 11 October, more than 6 months after the first experiment. Again the behaviour of the two species was similar, each showing two peaks. However, the two modes were more widely separated than before, the first being between 25 and 30° C. and the second at about 10° C. In both experiments the maximum peak occurred very near 27° C., the temperature given as the optimum for the most rapid development of *O. surinamensis* from egg to adult according to the investigations of Back & Cotton (1926).

The preference curve for the carpet beetle (*Anthrenus verbasci*) started at 30° C., attained its greatest height at about 12° C. and then suddenly dropped to almost nothing at the cold end. Its choice was thus decidedly within the cold zone, below 15° C., but not against the end of the trough.

The temperature preference for the bean weevil (*Acanthoscelides obtectus*) fluctuated quite violently between 30 and 13° C. All that can be gathered from results of this nature is that the weevils avoided temperatures above 30° C. In the control these insects had a definite preference for the ends. Biscuit weevils (*Sitodrepa panicea*) had one peak at about 21° C. and another at 17° C., with most of the insects in a zone between 21 and 14° C. Here again the insects showed an end preference in the control at a uniform temperature. Adult *Laemophloeus turcicus* presented a rather undecided temperature-preference curve, extending from about 30 to 14° C., with a peak at 21° C. and another at 15° C. Most of the insects were gathered in the zones 28 to 21° C. and 17 to 14° C. The clothes moth larva (*Tineola biselliella*) was the only Lepidopterous insect used. Here a definite preference was shown for the cool zone, 20 to 14° C., with a peak at about 17° C.

The above four experiments were conducted during the early part of this

work in one of the large entomological laboratories where uniform light and constant temperature did not prevail as in the dark room which was used in all other experiments.

(*b*) *Soil insects* (Table 3)

In all experiments with soil insects the thermometers projected directly into the soil, or other medium, in the same way as when food was used. At the hot end of the gradient moisture was continually condensing on the glass covers and dripping back on to the soil. As a result the moisture content of the soil remained fairly constant throughout. Most of the soil work was done with wireworms because (*a*) they are a serious agricultural pest in England, and (*b*) they could be obtained in sufficient quantity.

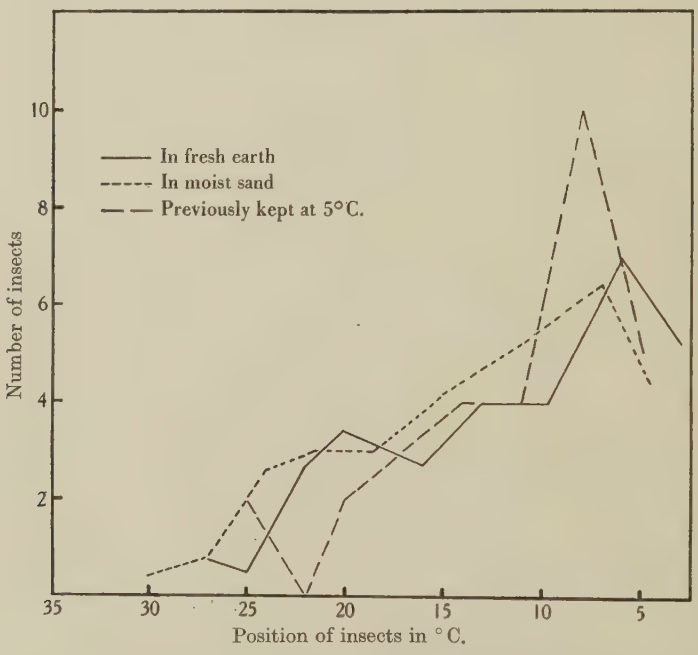

Fig. 9. Temperature-preference curve of wireworms, larvae of *Agriotes* sp. (Elateridae, Col.) under different conditions.

Fig. 9 shows a comparison between the results of wireworms that were placed in fresh earth (i.e. unmoistened) and those placed in well-moistened sand. As can be seen, about the only difference is that those in wet sand make a more gradual decline from a peak at the cold end (8–9° C.) of the gradient. In order to determine if previous temperature had any effect on their reactions a batch of wireworms was kept for 12 days at 5° C. After being placed in the gradient they were allowed ample time, 48 hr. to take up their preferred positions. From Fig. 9 it can be seen that the insects cover about the same range as when kept at room temperature. However, more individuals are

found at low temperatures, and there is a very abrupt dropping off from the cold end.

Ants (*Acanthomyops* sp.) were the second species of soil insects to be tried. They were also given fresh unmoistened earth and allowed to remain for 48 hr. before a reading was taken. In general their preference coincided with that of the wireworms, being highest at the cool end (8° C.) and gradually declining to about 30° C.

It is interesting that in none of the experiments with soil insects were they ever found to be most numerous at the very end of the gradient, their peak always occurring about 5–15 cm. from the cold end of the apparatus.

Table 3

Stage	Previous temp.	Medium	Temp. °C.	Relative humidity	Figure
Agriotes (Wireworms)					
L	Room	Fresh earth	(8)–20	—	9
L	Room	Moist sand	(8)–23	—	9
L	5° C.	Moist sand	(8)–18	—	9
Acanthomyops sp. (Ants)					
A	Room	Fresh earth	(10)–25	—	—
A	Room	None	(14)	30	—
Apanteles congestus					
A	Room	None	(10)–20	20–40	2, 3 and 10
Pteronides melanaspis					
L	Room	None	(11) and (31)	35 and 45	—
A (males)	Room	None	5–20	30–55	—
A (females)	Room	None	5–(8)–15	20–50	—
Dysdercus howardi (Cotton stainer)					
Nymph	Room	None	(12)–(25)	22–50	—
A	Room	None	12–25	22–50	—
Sepsidae (Diptera)					
A	Room	None	(9)	20	—
Forficula auricularia (Earwig)					
A	Room	None	(9) and 25–30	15 and 37–45	—
Cimex lecularius (Bedbug)					
A	Room	None	(12) and (22)	24 and 44	—

A = adult; L = larva.

Other insects (Table 3)

One day some small Braconid parasites were found in a cluster of spider's eggs. These were later identified by the British Museum as *Apanteles congestus* and proved to be one of the insects to give the most interesting results. The average for the 3 day experiment showed the parasites to have a decided preference for a temperature around 10° C. (Figs. 2 and 3). Here again the peak was 15 cm. from the end of the gradient, so one could hardly say that an end preference played a part in their reactions. It appeared that the insects' position shifted from day to day. The results were then plotted for each day separately, as shown in Fig. 10. On each successive day the parasites moved nearer and nearer to the cool end. The daily change in position is so definite that there can hardly be any doubt that they were actually moving to a cooler

region. An explanation as to why they successively moved from a warmer into a cooler region would be very difficult and could be a full-time problem in itself. Undoubtedly the Braconids underwent some fundamental physiological change.

At the same time that the experiment was started, eighteen surplus parasites, from the same egg mass, were placed in a vial and kept at room temperature. These were all dead after $1\frac{1}{2}$ days. After 3 days the experimental parasites, which were alive and quite active, were used in a control at a uniform

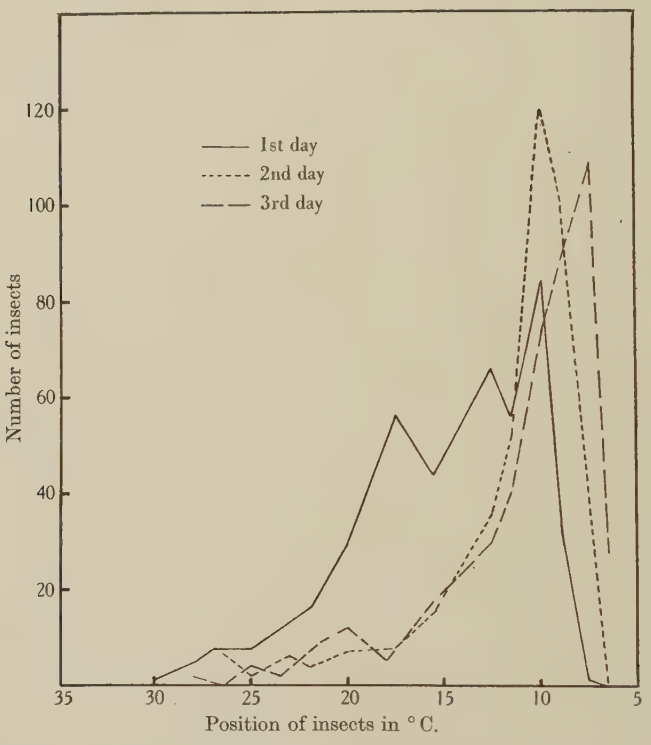

Fig. 10. Temperature-preference curve for *Apanteles congestus* for three successive days, showing the change in position towards the cool end of the gradient.

temperature. They gave a perfect random distribution throughout the gradient (Fig. 2). The methods followed in this experiment were slightly different from the normal. The parasites were not taken out of the gradient for feeding at night, but were allowed to remain in the apparatus continuously day and night. This was for two reasons: (*a*) the food of the Braconids was not known, and (*b*) the insects were too fragile to be handled any more than absolutely necessary.

A complete picture may be obtained of the behaviour of the saw-flies (*Pteronides melanaspis*), as the larvae can be compared with adults, and males

with females (Table 3). The larval preference went up very decidedly at 31° C., curved down, and then rose again at the extreme cold end of the gradient (11° C.). This is just opposite to the behaviour of the adult. Although they occupied the same temperature zone as did the larvae they rose in greatest numbers in the centre of the range (15–28° C.), rather than at the extreme temperatures near the ends of the zone. In comparing the differences between the two sexes it can be seen that they both extend over exactly the same range. However, the males are evenly distributed within this range, while the females are decidedly more numerous near the cool end (10–16° C.). The female saw-flies' choice for the second and third day was approximately the same, but for the first day greater numbers gathered at the lower temperatures.

Cotton-stainer nymphs (*Dysdercus howardii*) had a small peak at 29° C. and another at 25° C., but the majority were arranged between 25 and 12° C. The adults had a somewhat similar temperature range. These were tropical insects, imported from the West Indies, and one would expect to find more of them with a high temperature preference. Ants (*Acanthomyops* sp.), when given a choice of the gradient, without earth, repeatedly congregated directly against the cold end (14° C.). Those given soil, although they preferred the cool zone, were not found in large numbers tightly against the end, their peak appearing at least 15 cm. in from the end. Adult *Sepsid* flies present very much the same sort of preference as ants in an empty gradient, i.e. rising very sharply against the cold end (9° C.) of the trough. The end temperature here was about 5° lower than during the previous experiment.

The temperature preference for adult earwigs (*Forficula auricularis*) rises very suddenly at the cold end of the gradient. However, there is also a large number of insects gathered between 25 and 30° C. (Table 3). In this and the previous experiment the insects certainly did not gather at the cool end because of an end preference, as was readily shown by the controls. The bedbug (*Cimex lectularius*) preference, like that for the earwigs, goes up sharply against the cold end and also has a second peak near the centre of the gradient —about 22° C. (Table 3). However, the bedbug was not a suitable insect for experimental purposes, because its very strong thigmotropic tendencies were not easily overcome. The insects were inclined to gather in groups and when disturbed immediately formed another group regardless of temperature, except to avoid the very high temperatures.

6. DISCUSSION

It has been the purpose of this paper to show that, when given their choice of a temperature gradient, certain insects have a preferred temperature. The temperature range of all insects tested is shown and no effort has been made to select species to prove any particular case. It is realized that general conclusions cannot be drawn for insects as a whole from these experiments alone. However, it is believed that one conclusion is justified, namely, that insects

have a temperature preference, but it is a range rather than a point as suggested by some workers. The only preference some insects show is an avoidance of both extreme temperatures, e.g. the adult tobacco beetle when kept at room temperature, and horned flour beetle larvae in bran. On the other hand, they may merely avoid high temperatures and are to be found in all other parts of the gradient, e.g. the biscuit weevil, the bean weevil, rice weevil when kept at room temperature, adult *Dermestes* in food, and *Laemophloeus turcicus*. With insects that went to the cold end of the gradient it was difficult to distinguish whether they went there because of preference, or whether they wandered into the cold zone and were overcome, or trapped, before they could get away. Examples of such insects are the *Tribolium confusum* and *Calandra oryzae* when previously kept at 27° C., grain weevils, from both room temperature and 27° C., *Ptinus tectus* with and without food, ants and bedbugs.

Another rather peculiar preference is presented in the bi-modal curve with a peak near each end of the gradient. Saw-flies and earwigs are examples of this type. It has been suggested that these insects may have a wide range in which they are inactive, and are only active when they go outside of this zone. When they encounter too high a temperature they return to just within the upper limits of their preferred range. The same would happen when they encounter too low a temperature—they would return to just within the lower limits of their temperature zone. This is probably the explanation of a bi-modal curve with widely separate peaks.

In practice this would be what one might expect to find with most out-of-doors insects. It seems that it would be necessary for them to be indifferent to a fairly wide range of temperature in order to survive. Most summer insects must be able to withstand the hot days as well as quite cool nights. It is also not surprising that individuals of the same species sometimes give erratic and conflicting results in the temperature gradient when it is recalled that different individuals of the same insects, in nature, are often found at many different temperatures at the same time. Certain individuals may be in the hot sun while others are in the shade or other cool locations.

It might be said that insects go to a certain temperature in the gradient because they are attracted to the humidity there. The following insects have approximately the same temperature range both without and with food: *Dermestes* larvae, horned flour beetle larvae, meal-worms, tobacco beetles, rice weevils, *Ptinus tectus*, and *Tribolium* when previously kept at room temperature. Of course these are in addition to the soil insects, whose choice was also made independently of the relative humidity. The only insects that may have been trapped at the cold end were the ants.

One theory that may be advanced for insects gathering at the cold end of the gradient is they have *no* temperature preference, i.e. they were just wandering about, went into the cold zone, were overcome by the cold and

trapped there. In any case it is considered much more significant when insects show a preference outside of the cold zone.

No attempt was made to determine why an insect goes to or avoids a certain temperature. However, two theories which are worthy of mention are the classification of the insects' behaviour as follows: (*a*) behaviour reaction, in which insects receive the stimulus from a high or low temperature through certain receptors and their nervous system; (*b*) physiological reaction, in which the metabolic activities are speeded up, as when going into a higher temperature zone; or slowed down as when going into a lower temperature zone. In an insect that avoids a high temperature it would be impossible to tell whether it is showing a behaviour or a physiological reaction, without a detailed study of the insect's behaviour. On the other hand, an insect which avoids a low temperature is definitely showing a behaviour reaction. A study of the half-hourly and hourly observations from the daily record sheets shows that when insects leave the hot end of the gradient they invariably remain away from it. (After equal numbers have been introduced into the six thermometer openings.) However, they often move away from the cold end at first but eventually return to it and there remain.

It is possible that this temperature preferendum work may have definite practical applications as well as academic interest. Dr Baird, entomologist in charge of the Insect Parasite Laboratory, Belleville, Ontario, Canada, informs the writer that there all parasites, which are to be reared in large numbers, are tested for their temperature preference. They are then reared at their preferred temperature and much better results are obtained than formerly. It seems that the parasites do better at temperatures lower than those previously thought best for breeding purposes. The work has not yet been published. Temperature preference might also be used to advantage in eradicating insect pests, with a definite preferred temperature, from large warehouses and granaries where the temperature can be controlled. A small room, or other area, could be heated or cooled to the insect's preferendum while the rest of the building remained at an undesirable temperature. After the insects had gathered at their preferred temperature they could then be more easily destroyed.

During the course of the present work many questions and related problems have arisen to which a proper answer can only be given after further work and additional study have been carried out. One of the most important problems in connexion with temperature preferendum work, and one on which a large amount of work may be done, is: Why do insects seek out certain temperatures? What causes them to go to one temperature and not another a few degrees away? Another question almost equally important is: Why do certain insects, after being previously kept at a high temperature, have a lower preferred temperature than when previously kept at room temperature for the same length of time? In the future it is intended to concentrate mainly on the

preferendum of soil and aquatic insects. Here such variable factors as humidity, light and odour can be more readily standardized.

In the present experiment temperature has been considered the major factor in determining the position which the insects have taken up. However, such influences as humidity, odour, thigmotropism and possibly light must also be taken into account.

7. Summary

1. A description is given of three different types of apparatus experimented with before selecting a linear brass gradient which gave a range of temperature from 10 to 35° C. in a straight-line gradient. This allowed the insects a choice of about 1° C. in every 4 cm. The relative humidity in such an apparatus varied inversely with the temperature except where food was used, when it remained practically uniform.

2. The temperature preferendum was tested of twenty-three species of insects from six orders. Insects were chosen to represent different environments or habitats, such as the following: stored product insects, leaf-feeding insects, plant-sucking insects, human parasites, insect parasites and soil insects.

3. Results are based on experiments each carried out for not less than 3 days. In every case a control was also run for 1 day to get the random distribution of the insects.

4. At the cold end of the gradient the metabolic activities of the insects were slowed down to such an extent that many species were trapped there, thus giving an apparent preference for the colder end. As a result when insects went to a warmer zone it was considered more significant than when they went to a cold zone.

5. The flour beetle (*Tribolium confusum*) when kept at 27° C. had a lower preferred temperature than when kept at room temperature.

6. Wireworms kept at 5° C. for a fortnight gave no different reaction from those kept at room temperature.

7. Insects that were given food in the gradient had a narrower preference zone than when not given food.

8. In general the preferences of the immature forms tended to coincide with those of the adults of the same species.

9. With saw-flies (*Pteronides melanaspis*) the males tended to have a wider temperature range than did the females.

10. The Braconid parasites (*Apanteles congestus*) went to a lower temperature on each successive day they were in the gradient and at the end of 3 days were alive and quite active. At the same time a surplus stock kept at room temperature were all dead at the end of $1\frac{1}{2}$ days.

11. Generally speaking, all the insects experimented with have shown a definite temperature preference but the preference has been for a fairly wide range of temperature and not a point as has been suggested by some workers.

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REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 29, No. 2, August 1941)

The August number of the *Journal of Ecology* (Vol. 29, No. 2) contains ten original papers, notices of ecologcial papers received and the customary review of the *Journal of Animal Ecology*.

The original papers deal with a variety of subjects. J. Hope Simpson surveys the chalk grasslands of the South Downs, with special reference to grazing effects and to changes which have taken place since an earlier survey in 1920–21. Some of the more striking changes are recorded photographically. E. Pickworth Farrow contributes a short note on changes in the vegetation of Cavenham Heath. T. G. Tutin discusses the vegetation of the hydrosere, examining critically current concepts of the climax in this type of vegetation. In a similar short critical note, A. G. Tansley writes on the status of salt marsh vegetation in relation to the concept of formations.

Three papers deal with aquatic life conditions. Winifred Pennington describes work showing the effect of small animals (rotifers and *Daphnia*) in controlling the numbers of phytoplankton in small bodies of fresh water. Two papers by C. H. Mortimer deal with the thermal and chemical conditions in the deeper layers of the English Lakes, with special reference to the release of dissolved substances from mud to the water above it. An important new method is discussed, that of calculating eddy diffusion coefficients in the lowest layers of lake water.

Overseas vegetation is referred to in two papers. One, by R. C. Hoon and C. L. Dhawan, deals with the carbon-nitrogen ratios in the soil profiles of characteristic forest types in north-west Kashmir. A second, by A. S. Thomas, gives an account of the vegetation of the Sese Islands in Victoria Nyanza.

An especially notable feature of this number is the inclusion of the first part of the Biological Flora of the British Islands. This includes an introductory note outlining the plan and scope of the Flora and also accounts, by A. R. Clapham and P. W. Richards, of four species of *Juncus*, *J. conglomeratus*, *J. effusus*, *J. inflexus* and *J. subnodulosus*. These illustrate the method of approach and the material which it is hoped to include in the continuation of this work.

W. H. PEARSALL.

TROUT MANAGEMENT

Paul R. Needham (1940). *Trout Streams: conditions that determine their productivity and suggestions for stream and lake management.* 233 pp., 74 figs. and 36 tables. Comstock Publishing Company, 124 Roberts Place, Ithaca, New York. Price $3.00.

Of recent years the biology of the trout has been the object of scientific study in both Europe and America, and much information on the subject has been acquired; to some extent the management of trout fisheries has also been similarly investigated. Most of the knowledge thus gained about both trout and pisciculture is, however, distributed amongst various scientific and semi-scientific periodicals and is not therefore easily available. This consideration has led Dr Needham to produce a book which would bring together and

condense this scattered information and provide for the angler and the fishery manager an interesting account of the ecology and management of trout streams and one which would encourage their conservation. The author, who has himself done much ecological work on trout streams and on the productivity of such waters, has succeeded in producing a most clear and readable book and one which will be appreciated by not only those for whom it is intended but also by the professional biologist.

In America the term trout embraces the genera *Salmo*, *Salvelinus* and *Cristivomer*, the two last being scientifically char. The morphological characters which distinguish the nine 'trout' which come into one or other of these genera are noted and the distribution and habits of the fishes are described. The salmon of America, including five species of *Oncho-rhyncus* as well as *Salmo salar*, are treated in a similar way. The physical and chemical characteristics of streams are noted and discussed. Temperature is regarded as probably the most important factor governing the distribution of trout: the temperature range in American streams is considerable, and this factor thus operates there much more significantly than in British waters. The effect of oxygen and carbon-dioxide contents of the water on the fish are considered, the biology of pollution, is given in some detail, and a strong protest registered against the widespread 'open sewer policy' of stream management. There is no reference in this chapter, or elsewhere, to the growth made by trout in waters of different chemical composition. The growth reaction of trout to this factor appears to the reviewer to be one of the primary facts to be considered in connexion with trout culture.

The invertebrate fauna of the trout stream is described and figured in some detail, and interesting notes on the biology of the component organisms are given; many of the animals are similar in both genus and habits to those in British waters. An account of the food of the trout, consisting chiefly as it does of these stream organisms, is based on tables which show the stomach contents of trout captured throughout the year. The predominance of aquatic insect larvae in the diet of both brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) is similar to results obtained from *S. trutta* in this country. The fly-fisherman will find much of interest in these chapters on the fauna of the stream and the food consumed by the trout.

The author has done much stream survey work. The chapter on the distribution of trout food organisms reflects his intimate knowledge of the effect of those factors, such as the type of stream bed and the species and abundance of plants, which condition the productivity of running waters. His data on faunal distribution will interest the ecologist, and his assessment of the trout food produced by different environments is of special importance to the pisci-culturalist.

In America, as in this country, modern conditions have reduced the supply of trout fishing available to anglers. Attempts to return to the days of good fishing are being made through artificial propagation, stocking and protection of trout. It is pointed out that the stock of fish has been depleted by egg-taking from some rivers and returning but few of the resultant fry to the parent waters, and that domestic brood stocks should be substituted for the wild-egg sources. It is strongly advocated that scientific surveys of streams which would, amongst other things, assess the productivity of the water, are a necessary preliminary to sound stocking. It is also suggested that stricter size and 'bag' limit legislation is needed to help the recovery of depleted fisheries. The author points out that improvements in lake and stream must aim at providing shelter, food and good spawning grounds for the trout, and methods for fulfilling these objectives are set out. Finally, a plea is made for the co-operation of the angler, who by returning records of his catch will enable some assessment of the value of the conservation policy of the fishery to be made.

Trout streams, although naturally dealing with American fish and those problems affecting the management of American fresh waters, contains information and ideas that the British reader will find useful and interesting. The debt owed to England for information

about methods of stream improvement is acknowledged; we in our turn are chiefly indebted for this knowledge to fish culturalists and interested river-keepers, since the scientific study of the management of our lakes and rivers has received but little official encouragement. Dr Needham's book, and other publications which have come from across the Atlantic in the past few years, suggest that unless fishery management is promoted to a science in this country the debt he mentions will be owed in the reverse direction.

W. E. FROST.

WILDFOWL POPULATIONS

Anon. (1941). *Factors affecting the general status of wild geese and wild duck.* International Wildfowl Enquiry: Vol. 1, 123 pp. 22 figs. Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Price 10*s.* 6*d.*

A review of Vol. 2 in this series appeared in this *Journal*, Vol. 9, pp. 336–7. In the present volume some of the factors of the present era adversely affecting the numbers of wild duck and geese are considered. The main trend of events, discussed by P. R. Lowe in the introduction, is that ducks and geese mostly breed in the wilds of the north and then migrate to the more populated south. In the more primitive sporting days they conserved their numbers fairly well, but modern civilization is killing them off faster than they can reproduce. In the north, marshes are being drained, thus destroying the breeding grounds, and many more eggs (vast numbers in some cases) are being taken and breeding birds killed because, owing to cold storage and efficient transport, this has become a paying commercial proposition, rather than merely a means of helping out the food supply of the local inhabitants. Indiscriminate sportsmen go there, too, whereas the journey used to be too long and hazardous to tempt many.

In the south, both on passage and in winter quarters, a similar state of affairs now exists. Marshes are drained and rapid transport and efficient modern guns give the birds no respite. A drastic close season, based on scientific principles, is advocated. In Europe, at the moment, the legal duck shooting season opens when many of the young are but poor flyers and therefore there is a heavy drain on the young stock. It closes after the birds are already in breeding condition and, in many cases, paired. The U.S. Biological Survey estimated (1934) that only 18 to 20 million duck were left on the North American continent. 600,000 duck shooting licences were taken out, meaning less than forty birds for every licensed shooter. Not a moment too soon, the shooting season there 'has been limited to what amounts to one month only in the year for each state'. Fortunately things do not seem to be so serious on this side of the Atlantic.

In Chapter 2, first-hand information is given on some of the main northern breeding haunts of geese and ducks by C. G. and E. G. Bird, W. M. Congreve, S. W. P. Freme, C. T. Dalgety, J. H. McNeile, and E. S. Steward. North-east Greenland, owing to its inaccessibility, seems to be safe; but a gloomy picture is drawn of Iceland and Spitsbergen, where the commercial egg-gatherers are committing vast depredations on the nesting grounds. Usually, whole colonies are wiped out at a single visit and, in these high latitudes, a second hatching is improbable.

Chapter 3 is an extremely interesting discussion by R. W. Butcher on the distribution of *Zostera*. This, the so-called grass-wrack, eel-grass or wigeon-grass, really consists of three forms (*Z. marina*, *Z. marina* var. *angustifolia* and *Z. nana*) and is one of the main food plants of geese and ducks. It has been decreasing in quality for at least fifteen years, with a very marked drop in 1931 and 1932. After this date there has been some recovery in a few places, but mostly the decrease continues. The two most likely causes seem to be disease and a

change in the nature and stability of the substratum. An important part is played in the latter case by a cord-grass, said to have come from America, called *Spartina townsendii* (a true breeding hybrid between *S. stricta* and *S. alterniflora*). Butcher says: 'It is inevitable that reclamation by this grass would change the outline of an estuary and one of the plants that suffers most from the change is *Z. marina*. After establishing itself, *Spartina* consolidates the surrounding mud with its matted roots and then collects more and more mud, gradually raising a mud bank first above water-level, except at high tides, and ultimately above high-water mark so that a dry bank is formed where mud was before. As a consequence the river channel is narrowed and the currents are increased. This results in a removal of sand and mud away from the seaward edge of the *Spartina* zone and a permanent bed becomes a shifting one, and it has been pointed out that shifting sandy beds are uninhabited. There seems to be no doubt that in this way much of the *Zostera* has been exterminated, not by the cord-grass itself, but by the change the grass causes in the currents by its colonizing activities. *Zostera* can sometimes be seen in among the *Spartina*, but subsequently the latter forms a closed community when nothing else can grow.' He suggests that *Zostera* might be cultivated in artificially entrained lagoons and that alternative food plants should be encouraged—these being sea lettuce (*Ulva* and *Enteromorpha*), and *Ruppia*, *Zannichellia* and *Potamogeton pectinatus*.

The second half of the book is devoted to British decoys, by H. A. Gilbert and others (an average of 11,767 ducks per year are caught in such decoys); punt-gunning by C. T. Dalgety and others (each boat averages 1 to 15 birds per shooting day and there are 'not less than 105 working punts, nor more than 150, in England'); and migration data as the result of ringing. This last is by A. Landsborough Thomson and C. W. Mackworth Praed and includes interesting discussions, with many maps, of recoveries both in this country and abroad, which go a long way towards showing the status of our native birds and the origin of winter visitors. Both these subjects have, of course, to be well understood before one can draw up any intelligent laws of conservation.

In the last section, Miss P. Barclay-Smith summarizes all the protection laws for geese, ducks and 'sawbills' for the various European countries. This symposia by so many experts on the subject forms a most useful and readable book.

L. S. V. VENABLES.

ANIMALS AND FOREST REGENERATION

A. W. Moore (1940). *Wild animal damage to seed and seedlings on cut-over Douglas fir lands of Oregon and Washington.* U.S. Dep. Agric. Tech. Bull. No. 706, 27 pp. illustrated with photos. Superintendent of Documents, Washington, D.C., U.S.A. 5 cents.

This report opens with a vivid note on the reinvasion of old Oregon homesteads by fir trees that have begun in places to close the cycle of ecological succession after the original clearings were made in the tall forest. In the Douglas fir region of Oregon and Washington, forming only about 1·5 % of the acreage of the United States, there is 38 % of the available standing saw timber. The regeneration of these forests is therefore a matter of great importance, and the author notes that large parts of it are in poor condition as a result of the state in which the forests were left after logging. To the animal ecologist the special interest of this report lies in the notes upon the various seed eaters and tree damagers, and their biology and activities. Dearborn studied these as long as twenty years ago, and an attempt was then made to destroy or control the seed-eating rodents on sample areas, but with unsuccessful results for the reseeding.

The chief seed eaters are deer-mice (various species of *Peromyscus*) which range through a multitude of habitats. They are said to maintain numbers even in poor seed years, and to maintain themselves on alternative foods also on areas that have been logged. The trapping records used as an index of numbers are very slight statistically. Some cage experiments were made, in which various seeds were offered, and hemlock and Douglas fir were eaten, while certain others were less acceptable. Shrews are usually considered to be carnivorous, but it is shown that five out of the nine species present eat Douglas fir seed. Squirrels were not numerically important in the region studied, as they seek out the richer cone harvests elsewhere. Chipmunks (*Eutamias townsendii*) were generally distributed and feed in a similar way to the deer-mice, but as they hibernate, do not make heavy demands on the seed crop lying in winter. Birds, such as finches, are not very important during the winter season when the seed is most available, and their presence is regarded as partly beneficial on account of their partly insect-eating habits.

A careful trapping test, the methods of which are described in detail, was done on two plots of forest 200 ft. square, one on unburned and the other on burned 'slash', i.e. in this case forest that had had the smaller trees cut out, with resulting accumulation of cut branches on the ground. There were three times as many deer-mice on the burned as on the unburned, and ten times as many shrews on the unburned as on the burned. By marking the mice on the ears, it was proved that exchange sometimes took place between the two plots, which were about 340 yd. apart. This experiment, although inconclusive as a comparative test, owing to small numbers and the interchange of animals, illustrates the factors that enter into the planning of population measurements of this kind.

The animals that damage the young trees and seedlings are chiefly the redwood brush rabbit (*Sylvilagus bachmani ubericolor*), noted as attacking Sitka spruce; the Washington varying hare or snowshoe rabbit (*Lepus washingtonii*), attacking seedling plots of Douglas fir, with damage up to 35 % killed and nearly all nibbled eventually. The cottontail (*Sylvilagus nuttallii*) is thought to be of minor importance to the forest regeneration. It is noted that rabbits seem to have a preference for planted seedlings, a fact that has often been recorded also by foresters in Scotland, in connexion with vole damage to conifers. The so-called mountain beaver (*Aplodontia*) mows down a good deal of small vegetation, including young trees, in local patches, which become favoured haunts of the black-tailed deer (*Odocoileus hemionus columbianus*). These do a certain amount of browsing damage, as also the elk (*Cervus canadensis roosevelti*). The author remarks that he has not found much correlation between population density of animals and the damage that they do, probably because the local conditions determine so very much whether a particular food becomes important, and the density of that food whether the damage becomes a serious factor in forest regeneration.

The facts contained in this report, which is little more than a thorough reconnaissance that has raised a variety of further problems for investigation, illustrate well the niches of seed and tree-eating mammals and birds in the forest economy, and the openings that exist for combined study of density of population and habits of particular sections or colonies of it. Most of our State-planted forests in this country are too young to be seriously depleted by the demands of the present World-War, and when they grow up there will be hundreds of thousands of acres of conifers, occupying widely differing types of country, and inhabited by varied animal communities. Already the severe pressure of vole damage has been felt on the seedling trees and even on specimens up to eight years old or more. We know that the red squirrel has in the past done heavy damage to adult pines in Scotland, while both red and grey squirrels attack leading shoots of young conifers. Taylor (this *Journal*, Vol. 8, pp. 6–9) has recorded the recent multiplication of our three established species of deer in British woodlands and heaths, as well as three Asiatic species introduced into the country for amenity. Both Watt and Moore have proved the importance of rodents, mainly mice

and voles, in preventing or greatly reducing the regeneration of beech and oak woods in the south of England. It is to be hoped that forestry zoologists will not fail to adopt the new methods for collecting and studying live rodent populations in the field, that are being so rapidly evolved in America, U.S.S.R. and in this country.

CHARLES ELTON.

THE NATURAL HISTORY OF ISLANDS

F. Fraser Darling (1940). *Island years.* 306 pp., many photos, and 5 maps. G. Bell and Sons, York House, Portugal Street, London, W.C. 2. Price 12*s.*

Those who believe that the subject of ecology should be concerned with something more than a cold appraisal of the flow of energy and edible matter through the channels of plant and animal organisms, or of the regulating influence of the physical and chemical environment upon the rate of this flow and the form of the channels, will find in this, as in previous books by the author, a thoroughly satisfying outlook upon the wild life that surrounds us, and that refuses to be treated solely as a scientific cross-word puzzle or as a horde of serious competitors in the struggle for a reasonable standard of existence. When one tries to think of British naturalists during the last fifty years who have been able to approach wild animals with the proper spirit of respect and dignity, and with some consciousness of their extraordinary mystery and complexity, one is left with W. H. Hudson, and a few lesser writers like Richard Jeffreys. The rest seem often to suffer from condescension, sentimentalism or ignorance.

The reason why Fraser Darling's descriptions of animal life seem real and refreshing is that they avoid these common faults, and at the same time he is such a keen and patient observer that he really has something to say about the animals that is scientifically worth reading, even if (no doubt intentionally) he does not cast his results in the form of tables of figures and enormous lists of references. In the present book he summarizes a long series of experiences of field study on different Scottish islands; the Summer Isles (especially Eilean a' Chleirich), the Treshnish Isles, and North Rona; as well as on the mainland of the West of Scotland. The photographs of sea-birds and scenery are very beautiful, and the whole book is a vivid reminder to those ecologists who are pegged down to less pleasant regions or jobs, of the passion for natural history that normally drives them on to the study of their subject, and the need for finding a place for ecological attitudes in our system of education.

CHARLES ELTON.

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W.1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, B. M. Hobby, M. Mare, Barrington Moore, F. T. K. Pentelow, H. N. Southern and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

	PAGE
1. Ecological surveys and the relations of animals to habitat conditions	363
(*a*) Marine and brackish	363
(*b*) Fresh water	365
(*c*) Land	366
(*d*) Small islands	369
2. General reports and taxonomic studies of use to ecologists	369
3. Parasites	370
4. Food and food habits	371
5. Population studies	373
6. Migration, dispersal and introductions	374
7. Reports of organizations	375

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS HABITAT CONDITIONS

(*a*) Marine and brackish

Lysaght, A. M. (1941). 'The biology and Trematode parasites of the Gasteropod *Littorina neritoides* (L.) on the Plymouth breakwater.' J. Mar. Biol. Ass. U.K. 25: 41–67.

The distribution of *L. neritoides* is related to its response to light, gravity, moisture and shelter. Avoidance of wave exposure is thought to be of great importance, leading to the choice of a habitat covered only by spring tides. Spawning occurs at times of spring tides in the winter months and the fortnightly rhythm is maintained even when individuals are submerged. The occurrence of eggs and larvae in the plankton was studied. Settlement occurs in situations too exposed for the adults. Growth rates and sizes of maturity are given and also the extent and effect of parasitism by four species of trematodes.

Pierce, E. L. (1941). 'The occurrence and breeding of *Sagitta elegans* Verrill and *Sagitta setosa* J. Müller in parts of the Irish Sea.' J. Mar. Biol. Ass. U.K. 25: 113–24.

It is established that Liverpool Bay is a permanent habitat of *S. setosa*; two main breeding periods occur. *S. elegans* is predominant near Port Erin, where it has a single breeding period.

Rees, G. (1941). 'The resistance of the flatworm *Monocelis fusca* to changes in temperature and salinity under natural and experimental conditions.' J. Anim. Ecol. 10: 121–45.

A small pool on a cliff at Aberystwyth, containing only one litre of water, 8·32 ft. above high-water neap tides, and supplied by splashing, fluctuated in temperature from −1 to 28° C. and in salinity from 26·02 to 64 °/$_{oo}$. In the laboratory the salinity range for survival of *M. fusca* was 5·6–76·8 °/$_{oo}$, and the maximum temperature was 44·5° C.

Beadle, L. C. & Cragg, J. B. (1940). 'Studies on adaptation to salinity in *Gammarus* spp. I. Regulation of blood and tissues and the problem of adaptation to fresh water.' J. Exp. Biol. 17: 153–63.

Blood osmotic pressure and chloride and tissue chloride were determined when species of *Gammarus* were transferred to various dilutions of sea water. Blood of the marine *G. obtusatus* and *G. locusta* remains very hypertonic down to the respective limits of their tolerance: 50 and 25 % sea water. The brackish *G. duebeni* can tolerate almost the complete range of sea water dilutions, while the freshwater *G. pulex* can stand up to about 40 % sea water.

Ellis, W. G. (1939). 'Comparative measurements of water and electrolyte exchange in a stenohaline and in a euryhaline Polychaete.' J. Exp. Biol. 16: 483–6.

Nereis diversicolor is adaptable to brackish water; *Perinereis cultrifera* swells up and bursts. *N. diversicolor* is much better able to get rid of its salt and does so at a greater rate the more water it takes in.

Gohar, H. A. F. (1941). 'Weighing living marine animals.' Nature, Lond. 147: 177.

Marine animals are hard to weigh, chiefly because of the water contained in internal cavities open to the exterior. A method of weighing is suggested: the animal is weighed in normal sea water of known specific gravity, then in a medium of slightly higher or lower specific gravity. The differences in weight and specific gravity can be equated to the volume and the volume to the weight in air.

Lowndes, A. G. (1941). 'Weighing living marine animals.' Nature, Lond. 147: 298.

If the specific gravity of sea water is changed, osmosis may produce unknown effects on the animal's density. A method involving such effects is not therefore permissible: a displacement method is more satisfactory.

Bidder, G. P. (1941). 'Weighing living marine animals.' Nature, Lond. 147: 328–9.

Experimental evidence that change of osmotic pressure considerably affects the weight of an animal. One *Nereis* when transferred from 100 to 25 % sea water increased 135 % in weight after 22 hr.

Robertson, J. D. (1939). 'The inorganic composition of the body fluids of three marine invertebrates.' J. Exp. Biol. 16: 387–97.

The perivisceral fluid of the sea urchin (*Echinus esculentus*) is in complete physico-chemical equilibrium with the surrounding sea water. However, the blood plasmas of the lobster (*Homarus vulgaris*) and crab (*Cancer pagurus*) are maintained in dynamic equilibrium, having more Na, K and Ca and less Cl, Mg and SO_4 than sea water.

(*b*) Fresh water

Jones, J. R. Erichsen (1941). 'The fauna of the River Dovey, West Wales.' J. Anim. Ecol. 10: 12–24.

The purpose of this general ecological study of the virtually unpolluted Dovey is to provide a comparison with the lead and zinc polluted rivers Rheidol and Ystwyth, already studied. The fauna is rich and varied, comprising about 132 species, and fishing is excellent for salmon, sewin and trout. The greater richness of the Dovey fauna is largely due to lentic species unable to exist in the shallow, swift flowing Ystwyth devoid of vegetation.

Peach, F. E. R. (1939). 'Birds of the fenland.' Bird Notes & News, 18: 198–204.

A short account of the avifauna since draining took place. This was not completed until the nineteenth century, so that the disappearance of many species was sudden. Most records are about birds with a market value: protection had to be given to duck and geese in the sixteenth century before draining was attempted because such large numbers were decoyed. Waders such as avocets, ruffs and godwits mostly disappeared directly on account of the drainage, and concurrent increase in small species is noted, corn bunting and sedge warbler being especially abundant.

Wingfield, C. A. (1940). 'The effect of certain environmental factors on the growth of brown trout (*Salmo trutta* L.).' J. Exp. Biol. 17: 435–48.

Growth, in experimental tanks, was limited by temperature and not by food, which was provided in excess. With increasing temperatures the rate of increase in weight (per g. starting weight) was hyperbolic; with falling temperatures, linear. Below 6° C. no growth occurred. The width of the scale rings showed no change throughout the year, i.e. they did not vary with the different rates of growth of the fish, but remained constant, because food was always in excess of the metabolic requirements. In nature these requirements are not met during the winter and narrow rings are laid down. This is probably not because food is scarce but because it is less available: for example, to a fish inactivated by the low temperatures.

Ellis, W. G. & Jones, J. W. (1939). 'The activity of the spermatozoa of *Salmo salar* in relation to osmotic pressure.' J. Exp. Biol. 16: 530–4.

The sperms of salmon survive far longer in sea water of optimum concentration 20 % than in river water, in which they are very quickly inactivated. This is not because of an activating effect of the electrolytes in sea water, as sucrose solutions of equivalent osmotic pressure give the same increased survival. Sperms live even longer in egg fluid. The ejected sperm must probably meet the egg quickly unless it has the power of being reactivated after an interval in the river water.

Kaufmann, R. R. U. (1941). 'A contribution towards the list of aquatic Coleoptera of Hertfordshire.' Ent. Mon. Mag. 77: 33–5.

A list of water-beetles from Totteridge and Lea, with indications of month of capture and abundance.

Coe, R. L. (1941). 'Distribution of *Eristalis abusivus* Collin (Dipt., Syrphidae) in the British Isles, with notes on the female.' Ent. Mon. Mag. 77: 130–1.

This recently recognized fly is now recorded from 30 widely distributed localities and has evidently been overlooked on account of its close resemblance to the common *E. abustorum*.

Lloyd, B. (1941). 'A mass emergence of the dragonfly *Coenagrion puella*.' Entomologist, 74: 113–14.

In Hertfordshire on a hot sunny day, 22 May 1938, about 100 dragon-fly nymphs were observed within an hour and a half, clasping stems of plants above water-level, ready to emerge. Many were seen to hatch.

McClean, W. N. (1940). 'Windermere Basin: rainfall, run-off and storage.' Quart. J. R. Met. Soc. 66: 337–62.

Discusses (i) the characteristics of the area and scheme of hydrological stations, (ii) rainfall at the gauges and methods of assessing general rainfall on the area, (iii) the run-off and storage of the Windermere Basin, (iv) examples of analyses of the records.

Jenkin, B. M., Mortimer, C. H. & Pennington, W. (1941). 'The study of lake deposits.' Nature, Lond. 147: 496–500.

Nineteen cores of deposits up to 6·5 m. long have been taken at depths from 3 to 65 m. in Lake Windermere. Animal remains were frequent in muds, but absent from clays. The same species of planktonic Cladocera occurred in the brown organic mud (0–4 m.), in the organic layers between the narrow clay bands (4–5·5 m.), and below this in the organic silts within the laminated clays. The species composition has shown little change since Glacial times.

(*c*) Land

Fitter, R. S. R. (1941). 'Effect of the war on bird life.' Nature, Lond. 148: 59–60.

Records on this subject have been collected by the London Natural History Society. Very few air raid casualities among birds were reported, though explosions cause disturbance and alarm (examples of heron, crows, gulls, green sandpiper, etc.). Also examples of no alarm shown (barn owl, swift). Gulls seen feeding on fish probably killed by bombs in the Thames.

Graham, M. W. (1941). 'Hymenoptera, Hemiptera, Neuroptera, Trichoptera, etc., in East Lincolnshire.' Ent. Mon. Mag. 77: 97–101.

Important additions to the county list.

Wright, A. E. (1941). 'The north-western race of *Aricia agestis* Schf.' Entomologist, 74: 76–84.

Account of habits, habitat and variation of the brown argus butterfly.

Cockayne, E. A. (1941). 'The habits of some British moths.' Amat. Ent. 5: 21–30.

Surveys some recently discovered life histories and habits of British moths.

Praed, C. W. Mackworth- (1941). 'Records of a New Forest moth trap.' Entomologist, 74: 6–12.

Gives description and figures of light trap with list of species taken.

Beirne, B. P. (1941). 'Four years' captures of insects in light traps in Ireland.' Ent. Rec. 53: 45–50.

310 species (28 %) of the total number (1106) of moths known to occur in Ireland were taken at Seaport and Killarny, 27% of these were rare, 19% occasional, 28% frequent and 25% common.

De Worms, G. C. M. (1941). 'Moths at heads of *Phragmites*.' Entomologist, 74: 19.

Flower-heads of the common reed prove very attractive to moths. See also **Bretherton, R. F. (1941)**, Entomologist, 74: 96.

Burrows, C. R. N. (1941). '*Iodis chrysoprasaria*, Esp.' Ent. Rec. 53: 33–6.

Notes on the life history of this emerald moth.

Clutterbuck, C. G. (1941). 'Notes on Lepidoptera at the Lizard in 1940.' Entomologist, 74: 121–3.

Distributional records.

Crowson, R. A. (1941). 'On the occurrence of northern and southern species of Carabidae in a section of the Weald.' Ent. Rec. 53: 8–10.

Ground beetles found around Tunbridge Wells are grouped into northern species (recorded from Scotland and Scandinavia, but not southern France or Italy) and southern species (whose range includes Italy and sonthern France and south Germany, but not Scotland or Scandinavia). Tables of the geological formations on which the beetles were found are then given and it is observed that nearly all of both northern and southern species are recorded from the Hastings beds; while the Lower Greensand, like the Chalk, has an unusually high percentage of southern forms.

Niblett, M. (1941). 'Some gall-causing sawflies in Surrey.' Entomologist, 74: 110–12.

Niblett, M. (1941). 'Some notes on the Cynipid genus *Andricus*. II.' Entomologist, 74: 14–18.

Notes on galls and their makers.

Collin, J. E. (1941). 'The British species of the Dolichopodid genus *Medeterus* Fisch. (Dipt.).' Ent. Mon. Mag. 77: 141–53.

These flies frequent tree-trunks, walls and posts. The larvae live in the galleries of bark-beetles, either as predators or scavengers, and the pupae are found under bark. A key is given.

Morley, C. (1941). 'The history of *Cicadetta montana* Scop. in Britain, 1812–1940.' Ent. Mon. Mag. 77: 41–56.

A complete survey of the history of the only British Cicadid since its discovery in Britain in 1812 to the present day.

Gunn, D. L. (1940). 'The daily rhythm of activity of the cockroach, *Blatta orientalis* L. I. Aktograph experiments, especially in relation to light.' J. Exp. Biol. 17: 267–77.

Total daily activity as measured in a recording cage was the same in continuous light or darkness or in alternating light and darkness. In the latter case the period of greatest activity within the day was very strongly conditioned by light and could be made to start immediately continuous light was removed and at any time of day. This rhythm persisted for a while after a return to continuous light or darkness; but eventually activity became evenly distributed throughout the 24 hr.

Morison, G. D. (1941). 'Notes on earwigs in Northern Scotland.' Ent. Mon. Mag. 77: 128–30.

The author found earwigs in Kincardine, Aberdeen and Inverness-shire and all counties north of these on the mainland, also in the islands of Shetland, Skye, Lewis, Harris, N. and S. Uist, Benbecula and Barra. They occur from the seashore to the furthermost inland and up to at least 1000 ft. above sea-level, and are often common. Males with large forceps occurred most commonly along the coast of the mainland and islands, and males with smaller forceps were about equally common everywhere. Adults of both sexes pass the winter (October–March) in sheltered places under soil, stones, bark or dead leaves. They do not move about much in their winter quarters, and they eat very little, with intervals of many days between meals. Before and during spring mating occurs, the sexes coupling frequently. The male seems remarkably constant to the female, often remaining near the nest of eggs. The female usually digs a cell in the earth, where she lays 20–50 eggs, which she tends carefully. The nymphs live with their mother till they are about half or three-quarters grown, when she usually dies (about July). They often eat her dead body. The family seeks food at dusk, and probably at night, returning in the morning to pass the hours of daylight hidden in or near the nest. As the nymphs grow older each tends to wander farther afield alone. Before the insects are adult they seem fairly widely dispersed. There is one generation in the year.

Dicker, G. H. L. (1941). 'Notes on some Hemiptera-Heteroptera taken in the Reading district during 1940.' Ent. Mon. Mag. 77: 101–4.

Distributional records with some ecological notes.

Jacob, F. H. (1941). 'The over-wintering of *Myzus persicae* Sulz. on Brassicae in North Wales.' Ann. Appl. Biol. 28: 119–24.

The aphis *M. persicae* overwinters as apterae on species of *Brassica* out of doors under favourable conditions, and glasshouses form a reservoir from which numerous *M. persicae* may migrate in spring and early summer. Probably years of high infestations follow winters when widespread hibernation on *Brassica* has occurred, and vice versa.

Glasspoole, J. (1941). 'Mean temperature over the British Isles.' Quart. J. R. Met. Soc. 67: 47–51.

A correction of 1° F. for 300 ft. of altitude is applied to published records to obtain corresponding mean temperatures at sea-level. Estimates of the general mean temperature are then made by taking the mean of the values for 100 stations selected to give as uniform a distribution as possible.

Welmore, E. B. (1941). 'Thermal conductivity of soil.' Quart. J. R. Met. Soc. 67: 38.

Rate of change of temperature under a given gradient (whether on heating or cooling) is higher for sand than for clay and it is this property which gives to the former soil its characteristic 'warmth', although it leads to more rapid cooling under the influence of a fall in the atmospheric temperature.

Glasspoole, J. (1941). 'Variations in annual, seasonal and monthly rainfall over the British Isles, 1870–1939.' Quart. J. R. Met. Soc. 67: 5–14.

The general trend of the variations is shown by diagrams of ten-year means for each month, based on the similar statistics for England and Wales, Scotland and Ireland separately. Similar diagrams are given to show variations for the winter half-year, summer half-year and seasonal year separately.

Crowe, P. R. (1940). 'A new approach to the study of the seasonal incidence of British rainfall.' Quart. J. R. Met. Soc. 66: 285–316.

Rainfall records for the period 1881–1930 of 70 British stations, and records for the period 1831–80 for 12 stations, are analysed by a method of direct comparison of monthly values which does not involve the calculation of means. The rainy period was the same length in the first half century, but occurred earlier in the year.

Penman, H. L. (1940). 'Meteorological and soil factors affecting evaporation from fallow soil.' Quart. J. R. Met. Soc. 66: 401–10.

The mean daily rates of evaporation from a block of fallow soil at Rothamsted are examined for 94 periods varying in length from 13 to 45 days. It is shown that an almost complete description of evaporation can be obtained in terms of rainfall only, the nature of the correlation varying from season to season. A general treatment is attempted in physical terms, considering evaporation as due to diffusion across a non-turbulent boundary layer whose thickness is determined by wind velocity, the soil surface being assumed to be continuously at 100% R.H.

Lloyd, D. (1940). 'Evaporation-loss per month over drainage areas, II: loss over three areas.' Quart. J. R. Met. Soc. 67: 33–8.

Variations in loss can be largely associated with rainfall and temperature. The loss increases as the sub-surface has increasing permeability.

Manley, G. (1941). 'Observations of snow-cover on British mountains.' Quart. J. R. Met. Soc. 67: 1–4.

Gives table of days with snow-cover for Cairngorms, west-central Highlands, south-west Scotland, Lake District, north Pennines, north-east Pennines and Breconshire. An annual frequency of upwards of 100 days at 2000 ft. and at least 160 days at 3000 ft. is to be expected on Deeside and Speyside.

Callender, G. S. (1940). 'Variations of the amount of carbon dioxide in different air currents.' Quart. J. R. Met. Soc. 66: 395–400.

Discusses causes of variations of carbon dioxide in different air currents, seasonal variation, and presents observations showing that the amount of this gas in the air has increased since 1900, probably owing to the combustion of large amounts of coal and oil.

(*d*) Small islands

Harrison, J. W. Heslop (1941). '*Clostera pigra* Hufn. (Lep., Notodontidae) in Eilean Ornsay.' Ent. Mon. Mag. 77: 38.

The occurrence of this moth supplies another zoogeographical link in the chain connecting the Tiree-Coll group of islands with southern members of the Outer Isles.

Harrison, J. W. Heslop (1941). 'The Hebridean distribution of *Cerura furcula* L. (Lep., Notodontidae).' Ent. Mon. Mag. 77: 38.

This moth occurs in South Rona, Raasay and Soay (regarded as detached portions of the adjacent mainland) also on Coll. The latter is significant inasmuch as the affinities of the Coll flora and fauna lie towards those of the Outer Isles.

Harrison, J. W. Heslop (1941). 'The range and status of *Pieris napi* L. (Lep.) in the Outer Hebrides.' Ent. Mon. Mag. 77: 20.

Stresses that this butterfly is a genuine native in the Hebrides and not a migrant.

Harrison, J. W. Heslop (1941). 'More Hebridean days. II: The Isle of Benbecula.' Entomologist, 74: 1–5.

Includes lists of water-beetles and water-bugs and discursive notes on various other insects.

Harrison, J. W. Heslop (1941). 'More Hebridean days. III: The Isles of Tiree and Gunna.' Entomologist, 74: 97–100.

Further discursive notes.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Nuttall, G. H. F. (1940). 'Notes on the preparation of papers for publication in the *Journal of Hygiene* and in *Parasitology*.' J. Hyg., Camb. 40: 1–62.

Ecologists, too, would be well advised to study these notes: many manuscripts show the need for this sort of technical information.

Ford, E. (1941). 'Vertebral variation in teleostean fishes. II. The herring (*Clupea harengus* L.).' J. Mar. Biol. Ass. U.K. 25: 151–72.

This paper is a study of morphological characters which may be used to distinguish 'biological groups' of fish known to spawn in a definite area and season from year to year. Knowledge of the number and shape of the vertebrae and the extent to which individual variation may be expected in statistical samples is necessary to the development of adequate methods of characterizing shoals. The recording of all particulars for each fish on a card facilitates the analysis of data.

Farrell, A. F. O' (1941). 'The genitalia of Lepidoptera.' Amat. Ent. 5: 33–8.

A short account of these structures intended for the beginner.

Tams, W. H. T. (1941). 'Some British moths reviewed.' Amat. Ent. 5: 1–20.

Reviews advances made in knowledge of British Macrolepidoptera during recent years, the notes being illustrated with 73 figures (mainly of genitalia) and four plates.

Littlewood, F. (1941). 'On rearing Lepidoptera.' Entomologist, 74: 88–94, 101–6 & 124–30.

Useful practical hints.

Hinton, H. E. (1941). 'The Ptinidae of economic importance.' Bull. Ent. Res. 31: 331–81.

A taxonomic study of importance to ecologists studying stored products.

van Emden, F. I. (1941). 'Larvae of British beetles. II. A key to the British Lamellicornia larvae.' Ent. Mon. Mag. 77: 117–27.

Hinton, H. E. (1941). 'A key to the British species of *Holoparamecus* Curtis (Col., Lathridiidae).' Ent. Mon. Mag. 77: 131–2.

These beetles are of economic importance as they occur in corn and flour.

Macan, T. T. (1941). 'A key to the British water bugs (Hemiptera-Heteroptera, excluding Corixidae). With notes on their ecology.' Sci. Publ. Freshwater Biol. Ass. No. 4: 1–36.

With Sci. Publ. No. 1 (Corixidae) the two pamphlets cover all the British water-bugs. Ecological notes refer mainly to the Lake District.

Yarrow, I. H. H. & Guichard, K. M. (1941). 'Some rare Hymenoptera Aculeata, with two species new to Britain.' Ent. Mon. Mag. 77: 2–13.

Includes amendment to Perkin's key to British species of the bees *Andrena* and a new key to species of the bees *Lindenius*.

Edwards, F. W. (1941). 'Notes on British Heteropezinae, with description of a new genus (Diptera, Cecidomyiidae).' Proc. R. Ent. Soc. Lond. 10, B: 1–7.

These midges have gregarious larvae which live under bark and reproduce by paedogenesis.

Edwards, F. W. (1941). 'Notes on British fungus-gnats (Dipt., Mycetophilidae).' Ent. Mon. Mag. 77: 21–32 & 67–82.

Additions and corrections to the British list of fungus-gnats, excluding the Sciarinae.

3. PARASITES

Parkin, E. A. (1941). 'Symbiosis in larval Siricidae (Hymenoptera).' Nature, Lond. 147: 329.

Adult female woodwasps (*Sirex gigas, S. cyaneus*) carry a symbiotic Basidiomycete fungus, the oidia of which are transferred to the wasps' eggs. The fungus then infests the wood and lives independently, but is eaten by the tunnelling larva. The fungus, *Sterum sanguinolentum*, has also been found in special organs in the larvae (probably in the females only); but is absent from the pupal stage.

Freeman, R. B. (1941). 'The distribution of *Orchopeas wickhami* (Baker) (Siphonaptera), in relation to its host the American grey squirrel.' Ent. Mon. Mag. 77: 82–9.

The flea *O. wickhami* was first recognized in Britain in 1924. It is more or less specific to the American grey squirrel (*Sciurus carolinensis*). A list of the known records is given. Introduced with the squirrel at Woburn, Bedfordshire, in 1890, and probably with other American introductions, it has been found in several isolated centres to which the squirrel has been taken from these original colonies. In certain areas it has not been found, though looked for, and such absence may be attributed to absence from the original squirrel stocks from which these areas have been colonized rather than to any physical factors making such areas unsuitable. The percentages of infestation and flea index for all species of fleas are related to the breeding cycle of the squirrel. The grey squirrel is also parasitized by *Monopsyllus sciurorum*, the usual flea of the indigenous red squirrel (*Sciurus vulgaris*) and by several bird and mammal flies; these are often found, whether *Orchopeas wickhami* is present or not. A list of such records is given.

Collier, A. E. (1941). '*Pieris brassicae* 1939 and 1940.'

In 1939 at Weedon very few larvae were stung by parasites, but in 1940 practically all were attacked.

Lloyd, D. C. (1939). 'A study of some factors governing the choice of hosts and distribution of progeny by the Chalcid *Ooencyrtus kuvanae* Howard.' Phil. Trans. Roy. Soc. B, 229: 275–322.

Unparasitized eggs of the gipsy moth (*Porthetria dispar*) and those containing various stages of the parasite from egg to pupa were exposed in Petri dishes. Oviposition was not at random, but showed a graded response correlated with the decreasing quantity of host material. If only parasitized host eggs were available this Chalcid tended to retain her eggs rather than be obliged to superparasitize the host.

4. FOOD AND FOOD HABITS

Summerhayes, V. S. (1941). 'The effect of voles (*Microtus agrestis*) on vegetation.' J. Ecol. 29: 14–48.

This study, carried out from 1932 to 1939, in conjunction with the Bureau of Animal Population, Oxford University, and with the assistance of the Forestry Commission, on the State Forests of Newcastleton, Roxburghshire, Scotland, and Corris, Merionethshire, Wales, by a comparison of fenced and control areas, showed that the voles reduce the luxuriance of the dominant grasses both by feeding on them and by loosening the roots and surface humus, thereby favouring the increase of mosses and non-dominant plants.

Southern, H. N. & Watson, J. S. (1941). 'Summer food of the red fox (*Vulpes vulpes*) in Great Britain: a preliminary report.' J. Anim. Ecol. 10: 1–11.

This is a side investigation of a wild rabbit population study, and includes qualitative analyses of 40 stomach contents and 18 faecal pellets, of which 26 were from Wales, 25 from the 'Plain' (Oxfordshire, Berkshire and Goucestershire) and 7 from Scotland. Rabbits were the commonest food (55%), followed by sheep (mostly in Wales), small birds, and insects.

Hosking, E. J. (1941). 'Some notes on the long-eared owl.' Brit. Birds, 35: 2–8.

Close watching at a nest with young for five days after hatching gave the following list of prey identified: 19 rats, 7 field-mice and 2 field voles.

Allen, K. R. (1941). 'Studies on the biology of the early stages of the salmon (*Salmo salar*). 2. Feeding habits.' J. Anim. Ecol. 10: 47–76.

The feeding habits of first-year and second-year salmon in the Eden river in northern England and the Thurso river in northern Scotland were intensively studied by detailed comparisons between the animals found in the fishes' stomachs and the animals available for food in the fauna of the streams. The degree of selection exercised by a fish increases with the number of animals in its stomach. In the first-year fish nearly all the selected animals belong to the two most numerous groups, and in the second-year fish to the five most numerous groups. The evaluation of a fauna as a food supply for young salmon can be made by using the methods developed in this study to measure the availabilities of the different animals in the fauna.

Pentelow, F. T. K. (1939). 'The relation between growth and food consumption in the brown trout (*Salmo trutta*).' J. Exp. Biol. 16: 446–73.

Fish were kept in separate tanks and fed with known weights of *Gammarus pulex*. Some were given unrestricted quantities; others the bare minimum necessary to maintain weight. About 5 g. *Gammarus* produced 1 g. increase in weight: a highly efficient conversion of food, since about 2 g. of this was required for maintenance of weight. About 200–300 *Gammarus* were eaten per g. increase. Growth was slow in winter and at a maximum between 50 and 60° F. Appetite increased with temperature up to 60° F.

Hartley, P. H. T. (1940). 'The food of coarse fish: being the interim report on the coarse fish investigation.' Sci. Publ. Freshw. Biol. Ass. Brit. Emp. No. 3: 1–33.

Contains some useful advance information about the food of pike, eel, gudgeon and (in particular) roach, among other fish. Roach were predominantly vegetable feeders; the older fish eat a greater proportion of molluscs. Each fish appears to fast during part of the colder half of the year.

Butler, C. G. (1941). 'A study of the frequency with which honeybees visit red clover (*Trifolium pratense*), together with an examination of the environmental conditions.' Ann. Appl. Biol. 28: 125–34.

When the nectar concentration was lower than that of other honey plants and when the nectar was not high enough in the corolla tube, bumble-bees were usually more abundant than honeybees except at peak periods of pollen collection. Two peaks of honeybee activity were observed, about 10.30 a.m. and 3 p.m. (G.m.t.).

Butler, C. G. (1940). 'The choice of drinking water by the honeybee.' J. Exp. Biol. 17: 253–61.

Bees were trained to come for water to a table where their preference for various aqueous solutions were compared with that for distilled water. An important feature of these experiments was the exposure of the solutions in the form of the Latin Square: a modern statistical method for enabling the significance of an experiment to be checked immediately. Common salt in dilutions from $N/20$ to $N/80$ was preferred to distilled water. Greatest preference was given the distillate from rain water that had collected among dead leaves or on cow dung. Probably the bees were attracted by certain volatile substances, which, if absorbed on charcoal decreased the attractiveness of these sources of water.

Parr, W. J. & Speyer, E. R. (1941). 'Some observations on the life history of the angleshades moth (*Brotolomia meticulosa* L.).' Ann. Appl. Biol. 28: 29–33.

Includes list of food plants.

Hinton, H. E. & Stephens, F. L. (1941). 'Notes on the food of *Micropeplus*, with a description of the pupa of *M. fulvus* Erichson (Coleoptera, Micropeplidae).' Proc. R. Ent. Soc. Lond. (A), 16: 29–32.

The larvae and adults of *M. fulvus* and *M. staphylinoides* feed almost entirely on fungi, particularly the spores and conidia, and are probably never carnivorous. About 15 % of the conidia of *Penicillium* found in the faeces of the adults of *M. fulvus* had not been killed but were so affected that they germinated much more quickly than usual. *M. fulvus* is capable of the internal mechanical and external transmission of *Penicillium*. The pupa of *M. fulvus* is described.

Hardy, A. C. (1941). 'Plankton as a source of food.' Nature, Lond. 147: 695–6.

Discussion of the suggestion that marine plankton should be used as a supplementary food in war time. Analyses prove that the material is of high food value, and it is known that southern whales can reach lengths of over 60 ft. within two years from birth, on plankton food alone. The chief problem is of economic collection. The author suggests utilizing the tidal flow in west of Scotland sea lochs, where plankton is rich. Swing nets made of stramin fabric supported by ropes might yield 267 kg. or 5½ cwt. dry weight of plankton per ten nets per 12 hr., if each had an opening of 30 sq. m. A further argument for starting such an enterprise is the decrease in herring drift-net fisheries. Direct collection would cut out the fish stage. Nothing is said about the taste of plankton, except that a yachting party of eight consumed a meal of it fifty years ago.

Walker, E. (1941). 'Plankton as a source of food.' Nature, Lond. 147: 808.

Suggests use also of freshwater phytoplankton, which at times reaches a high density.

Gardiner, A. C. (1941). 'Plankton as a source of food.' Nature, Lond. 148: 115.

Although lakes and reservoirs may have high density of phytoplankton, this usually only lasts a short time in the season. Large-scale collection is very difficult owing to fine mesh of nets. Also a high proportion of the diatom plankton is silicon. Recommends concentrating on freshwater zooplankton which would be easier to collect. Samples from Lough Derg and Windermere were not unpleasant to the taste.

Gross, F. (1941). 'Food production by fish and oyster farming.' Nature, Lond. 148: 71–4.

Earlier trials of placing in the sea the larvae of fish from special hatcheries have not been conclusively proved to have much effect on the fish supplies. Transportation of young plaice from poor coastal waters to the Dogger Bank resulted in greatly increased growth rates. Wartime restrictions on fishing suggest the possibility of culturing marine fish and oysters artificially for food, as is successfully done with freshwater fish. The proposal is to undertake artificial marine plankton culture, transport small flat fish into ponds and rear them on bottom-living molluscs and polychaetes in turn dependent on the plankton or detritus derived from it. Strict control of density, and so far as possible, of cannibalism, would be essential. Some preliminary work on oyster culture has been done, and might be expanded. There are some speculations about costs.

5. POPULATION STUDIES

Parmenter, L. & Fitter, R. S. R. (1941). 'A spring census of the birds of Limpsfield Common.' Lond. Nat. for 1940: 19–20.

This was the first of a yearly April census of the resident bird population.

Colquhoun, M. K. (1941). 'The birds of Savernake Forest, Wiltshire.' J. Anim. Ecol. 10: 25–34.

An uncompleted quantitative survey showed 37 species which are recorded as numbers of adults seen per 10 hr. walking, by months from March to June, and by habitat, oak, oak and scrub, thorn scrub, and beech. Efforts by the Forestry Commission to secure natural regeneration of oak are adversely affecting insectivorous birds, and therefore indicate the need for co-operative research.

Colquhoun, M. K. & Morley, A. (1941). 'The density of downland birds.' J. Anim. Ecol. 10: 35–46.

Counts of individual birds made in the winter, pre-breeding and breeding seasons were corrected for conspicuousness, which was based on the greatest distance at which the largest number of a species could be identified. There were 12 species, and a density per 100 acres of 14, 35 and 32 for the three periods.

Alexander, W. B. (1941). 'The index of heron population, 1940.' Brit. Birds, 34: 189–94.

Records a decrease of 23 % in the nesting population of 1940, probably due to the severe winter.

Payne, L. G. (1940). 'The edible frog in England.' Discovery, 3: 41–3.

This species is doubtfully indigenous; it was common in Norfolk in the last half of the nineteenth century, but is rare now. They are present in London in at least two localities. The clusters of spawn are in small flat clumps, which distinguishes them from those of the common frog.

MacLagan, D. S. (1940). 'Sunspots and insect outbreaks: an epidemiological study.' Proc. Univ. Durham Phil. Soc. 10: 173–99.

Outbreaks of ague, antler moth (*Cerapteryx*), diamond-back moth (*Plutella*), leather-jacket (*Tipula*), turnip flea-beetle (*Phyllotreta*) and cutworm (*Euxoa*) have occurred at intervals of about 11 years. This periodicity is correlated with sunspot maxima.

Walker, G. T. (1941). 'Period hunting in practice.' Quart. J. R. Met. Soc. 67: 15–18.

For statisticians.

Barnes, H. F. (1941). 'Studies of fluctuations in insect populations. VIII. The wheat blossom midges on Broadbalk, 1932–40, with a discussion of the results obtained 1927–40.' J. Anim. Ecol. 10: 94–120.

The peak of emergence of *Contarinia tritici* is always from 4 to 24 June, that of *Sitodiplosis mosellana* 4 June to 1 July. The former can over-winter two years, the latter three years. Weather factors at certain periods influence the subsequent numbers of midges. There seem to be cycles of about five years of both midges, considered separately or together. Years of high relative parasitism follow years of high larval numbers and vice versa. Low relative parasitism accompanies high winter survival and vice versa.

Barnes, H. F. (1941). 'Sampling for leatherjackets with orthodichlorobenzene emulsion.' Ann. Appl. Biol. 28: 23–8.

The populations of leatherjackets per sq. yard of lawn for 1937–40 were 28, 17, 40 and 25 respectively.

Anon. (1941). 'Wireworms and newly-ploughed grassland.' 'J. Minist. Agric. 47: 251–7.

A population survey. There appears to be a steady reduction in the wireworm population from south to north and to some extent from east to west. 261 fields situated in the eastern, south-eastern, southern and midland counties have an average wireworm population of 738,000 per acre; 81 fields in the south-western counties, south and mid-Wales have an average figure of 347,000; while 131 fields in North Wales and the northern counties have an average population of 200,000 per acre.

Buckstone, A. A. W. (1941). 'Scarcity of *Gonepteryx rhamni* in Surrey.' Entomologist, 74: 12.

The author enquires if the brimstone butterfly was generally scarce in 1940, as he failed to observe a single individual during summer and autumn, although hibernated specimens were common in the spring.

Buckstone, A. A. W. (1941). 'Assembling of *Thecla quercus*.' Entomologist, 74: 5.

Records the capture of 17 purple hairstreak butterflies from a cloud disturbed from an oak branch at Ashtead, Surrey, in August.

Watkin, E. E. (1941). 'The yearly life cycle of the Amphipod, *Corophium volutator*.' J. Anim. Ecol. 10: 77–93.

By measuring all individuals in samples collected throughout 1938 and early 1939, and determining the sexual condition of females, it was found that the over-wintering population begins breeding in February. The next generation breeds in August and September. The average size of breeding females is around 7 mm. Males are smaller, and their proportion varies, being higher during breeding periods.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Bracken, C. W. (1941). '*Danaus plexippus* in North Devon.' Entomologist, 74: 42.

A female of the North American race of this butterfly was taken on 4 November 1940, at Putsborough, Georgeham, north Devon. It has not been seen in England since 15 August 1938, and never previously in November.

Dannreuther, T. (1941). 'Migration records.' Entomologist, 74: 54–62.

Discusses migratory movements of *Pieris brassicae* and concludes that 1940, like 1937 and 1939, may be regarded as another 'cabbage white year', for no other migrant species has been reported in large scale movement. Also includes records of insects at sea, and gives general summary of immigrant insect records for the year with table of comparative estimates of abundance and crude totals, references to phenological observations and to migratory locusts.

Burkill, H. J. (1941). 'British butterflies in 1940.' Lond. Nat. for 1940: 15–16.

Pieris brassicae (large cabbage white) were still quite plentiful, though perhaps less of a plague than during 1939.

Tulloch, J. B. G. (1941). 'Mass movement of *Pieris brassicae* and *P. rapae*.' Entomologist, 74: 32–5.

Suggests that these so-called 'migrations' are not migrations in the sense of bird and animal movements, which have to do with feeding or breeding, but are mass movements due to atmospheric disturbances.

Donisthorpe, H. (1941). '*Aulonium trisculatum*, Fourc., extending its range in England.' Ent. Rec. 53: 18–19.

First discovered at Enfield in 1904, this beetle has now reached Pilton, Northamptonshire.

Beaumont, A. & Staniland, L. N. (1941). 'The spread of eelworm in commercial plantings.' Ann. Appl. Biol. 28: 135–41.

Spread chiefly takes place in the surface water in the direction of the surface drainage.

Watkin, E. E. (1941). 'Observations on the night tidal migrant Crustacea of Kames Bay.' J. Mar. Biol. Ass. U.K. 25: 81–96.

Some species of small Crustacea perform simple vertical migrations at night into the intertidal waters; other species are brought in by the tide. Some of the former group maintain a zonation similar to that found in the sand. One predatory species probably makes both day and night migrations for feeding. Examination was made of the state of maturity of all species.

7. REPORTS OF ORGANIZATIONS

British Trust for Ornithology (1941). Seventh Report. 12 pp.

Records of progress are given for several field inquiries. The hatching and fledging data suggest that greater numbers of small Passerines were fledged in 1940 than in 1939. Ringing recoveries include two puffins and one great skua that made an east to west crossing of the Atlantic. New inquiries into nest sanitation, and reactions of birds to war conditions are being started.

Freshwater Biological Association of the British Empire. Ninth Annual Report for the Year ending 31st March, 1941. 53 pp.

Included in the report are accounts of research on eels, perch, minnows, char, trout, powan; the effect of fertilizers on production of fish in ponds, on invertebrates and algae; the interchange of dissolved substances between water and mud; the bottom deposits of lakes; the bacteriology of freshwaters; and coarse fish. Part of the Association's programme has been modified to meet immediate war-time needs and the experimental perch fishery is of particular interest in this connexion.

Yorkshire Fishery District, Seventy-Fourth Annual Report on the Salmon, Trout and Freshwater Fisheries in Yorkshire (1940) (by **R. W. Ward**). 32 pp.

The total catch of salmon in this Fishery District during 1940 was 544 fish weighing 8181 lb. and of migratory trout 2560 fish weighing 15,716½ lb. The catch of salmon was less than half that of the previous year. The Report also includes notes on fish passes; freshwater fisheries (excluding Salmonidae); the fish hatchery at Keld Head; and pollution. Pollution has not noticeably increased during the year.

Scottish Marine Biological Association. Annual Report, 1939–1940. 31 pp.

Experimental investigations have been made in the sea on factors influencing the vertical migrations of zooplankton. A brief report is given of the night migrant fauna of an intertidal habitat (see Watkin, 1941) and also of work on small Copepods and on the nutrient value of marine animals.

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